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Genetic Aspects of Mineral Metabolism in Sheep and Other Studies

by

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Contents

SUMMARY

The submission is in three parts.

Section 1, the main part, provides evidence of genetic variation in the concentration of copper in the blood, liver and brain of sheep and of breed variation in the incidence of disorders associated with copper metabolism. Evidence of a less detailed kind is also presented of genetic variation in the concentration of other minerals in the blood of both sheep and cattle. The studies also contribute information on the magnitude of several non-genetic sources of variation in mineral concentrations.

This work provides a basis for the hypothesis that heredity partly controls the nutritional requirements of ruminants for minerals, including 'trace' elements. It suggests that by taking the genetic variation into account it should be possible to formulate the nutritional needs of the animals more accurately than otherwise and thus help to optimise the efficiency of animal production. The work suggests that it may also be possible to breed animals for adaptation to mineral deficiencies or excesses, or for resistance to metabolic disorders. The work demonstrates, in this facet of animal production, the inter-relationship of genetics and nutrition in the maintenance of animal health.

Section 2, of the thesis deals with more general studies on cattle and sheep and is concerned with the apportionment of variation to genetic and non-genetic sources for a variety of traits related to performance and survival. Some of these experiments provided the initial genetic evidence, and later the necessary opportunities, for exploring variation in mineral metabolism.

Section 3 deals with the structure and dynamics of breed organisation and the way these affect the potential for genetic improvement of livestock. This work was undertaken before experimental facilities had become available to the author. Much of the data used for the cattle papers (Nos. 38-42) in this section contributed to the author's Ph.D. thesis in 1950.

ACKNOWLEDGEMENTS

The work in section 1 of the thesis was initiated by the author and developed primarily by him. The biochemical analyses of blood and tissues were undertaken by Dr. A.C. Field of the Moredun Research Institute. Mr. N.S.M. Macleod, lately of the Veterinary Investigation Centre, East of Scotland College of Agriculture performed the post mortem examinations used for one of the studies. Other collaboration, which is also acknowledged in the co-authorship of papers, involved primarily statistical and computer programming assistance.

Some of the work reported in Section 2 was collaborative but the author had primary responsibility for most of it. Any collaboration is acknowledged in the papers or by co-authorship.

One of the papers (No. 39) in Section 3 involved collaboration with its co-author. Much of the data used for the cattle papers (Nos. 38-42) in this section was previously used as material for a Ph.D. thesis.

PREFACE

Section 1: Genetic Aspects of Mineral Metabolism

Trace elements and other minerals have vital roles in animal health, growth, reproduction, milk and wool production. Intensified systems of animal production have drawn increasing attention to the penalties of deficiencies, excesses and imbalances of these elements. Animals vary in their responses to nutritional and management practices even when account is taken of, for example, age, state of pregnancy or level of milk production. Numerous studies of minerals in blood also bear witness to a large amount of variation in concentrations to be observed among individuals.

The papers in this section of the submission provide the first systematic evidence that the animal itself partly controls its responses to copper. There is also more tentative evidence that the animal's heredity plays a part in controlling the uptake or utilisation of other minerals. Until the genetic basis of this control is adequately understood it seems unlikely that it will be possible to formulate satisfactory predictions of the responses of animals to particular mineral regimes. The application of such knowledge is relevant to both intensive and extensive systems of animal production. On the one hand it may be possible to formulate the nutritional needs of animals more accurately in order to optimise performance. On the other hand it may become possible to breed animals for adaptation to particular situations of mineral deficiencies or excesses, or for resistance to metabolic disorders.

Copper in sheep

In 1965, the author found that the liability to a neurological disease of sheep ("swayback"), which is associated with copper metabolism, is partly under genetic control. The discovery arose from a chance occurrence of the disease, but within an experimental framework designed specifically for the study of genetic variation. The experiment in question involved a comparison of three breeds of sheep and their crosses and each of these at varying stages of inbreeding achieved by successive parent-offspring or full-sib matings. The breeds and crosses in question differed in a number of important aspects of their performance including growth, reproductive and maternal performance and lamb survival (see papers 30, 36, 37 in section 2). The sheep of the different breeds and crosses had been run as a single flock at grass for nine years at the time of the swayback outbreak and all the sheep involved had been born and reared on the farm. Corroboration of breed variation in the incidence of swayback was also obtained from another contemporary experimental flock in the Animal Breeding Research Organisation and some supporting evidence, previously neglected, was found in the records of a former experiment. The evidence (reported in paper No. 1) suggests strongly that the incidence of swayback is under some measure of genetic control as shown primarily by the differences in incidence among the breeds and crosses. Evidence also suggested, that the genetic variation was additive, since crossbred sheep had an incidence of the disorder almost half-way between that of the parental breeds, and inbreds did not differ in incidence from non-inbreds. This contrasts with the evidence for marked deviations from additive variation for lamb mortality in general (other

than that attributable to swayback). In this case, crossbreds survived better than expected from the mid-parental values and inbreds were considerably worse than non-inbreds (Table 4, paper 1). This points to dominance and epistasis as contributing to the genetic component of lamb mortality.

Since the breeds involved also differed in body weight it seemed important to test more rigorously the possibility that differences in the incidence of the disorder might be a function of body weight. Results of such an investigation are reported in paper No. 5 and show that breed differences in swayback incidence were important independent of body weight. The paper also adds a measure of statistical sophistication to the prediction of the probability of swayback occurring among lambs for the breeds and crosses involved and for a variety of circumstances.

Although out of chronological context, attention should here be drawn to the report of the effects of breed and other factors, such as body size, on the mortality rate of sheep following copper injection (paper No. 8). Such injections are commonly given to reduce the probability of an occurrence of swayback. On a simple, mechanistic view of the action of copper, poisoning might be regarded as the opposite of deficiency. Whilst this turns out to be too simplified a view, the evidence does point to the probability that breeds differ in their susceptibility to copper poisoning, and that this is in fact partly and inversely related to the susceptibility to swayback.

Following the finding of genetic differences in the incidence of swayback, collaboration was sought from the Moredun Research

Institute, and Dr. Field in particular, to study concentrations of copper in blood, liver and brain tissue of sheep of different genetic groupings which, for experimental purposes, were kept together under the same conditions of management and feeding. Papers derived from these studies form the major part of this section of the submission. The picture which emerges shows that a part of the very large amount of variation in copper concentrations found among individuals which has hitherto been unaccounted for can be explained by heredity (see in particular papers 2, 3, 4, 10, 11, 14, 16).

Not only do the concentrations of copper in blood, liver and brain tissue differ among breeds and among progeny groups of different rams, but the changes in copper levels of whole blood, observed by sampling at different times of year, were also found to show genetic variation (paper No. 9). The seasonal changes, however, were also influenced by pregnancy and by injecting sheep with prophylactic doses of copper in early pregnancy. A later investigation (paper 17) was therefore undertaken with young non-pregnant females at grass and without copper treatment. This corroborated the evidence for marked seasonal changes in copper levels of sheep at grass at this farm (though these are confounded with any changes attributable to age) and showed that breed differences were present at all stages. This study (paper 17) also showed that within breed groups the correlation between repeat observations of plasma copper levels of sheep, sampled at from 9 weeks to more than 3 years apart in time, was in the range 0.4 to 0.9.

There was clearly a positive association between levels of

copper in blood, liver and brain, and an inverse relationship of these with the incidence of swayback at the start of the investigational period, in respect of the three pure breeds, the Scottish Blackface, the Cheviot and the Welsh Mountain, used in several of the studies. The crosses, among these breeds, however, provide some further insights. Whereas for blood levels the crossbreds were fairly consistently at the level of the higher parent contributing to the cross, for liver concentration the crosses were either not significantly different from mid-parental levels when adult sheep were examined (paper No. 3) or, on average only slightly above, when estimated from the livers of lambs which had died (paper No. 16). For brain tissue, copper levels of crossbreds were close to the average of parental levels (paper 16). For swayback the incidence among the crosses was not significantly different from the average of the parental breeds involved (paper 1). Taken together, the evidence suggests some independence of copper levels in blood from those in liver and brain and from the incidence of swayback. Critical examination of the breed differences in copper levels in groups surviving a swayback outbreak compared with groups in years when swayback had not occurred (paper 13) showed, however, that swayback losses did affect the relative breed differences in blood copper levels of survivors and thus exerted some selective effect.

Whilst most of the observations on blood levels of copper were made on adult sheep the design of the main experiment did not allow a clear differentiation of genetic effects from the possibility of long-term carry-over effects of the genetically different maternal environment of these sheep. (For example, Scottish Blackface sheep had Scottish Blackface mothers whilst Blackface-Cheviot crosses had

parents which were themselves Blackface-Cheviot crosses, etc.). Breed type of lamb and maternal breed type were confounded. A study was thus undertaken in which this would not be so (paper No. 11). For lambs which were the offspring of different breeds of sire, the maternal breed contribution, both genetic and non-genetic, was either "constant" or "averaged out". Marked differences were, however, found in copper concentrations attributable to the breed of sire of the lambs when they were around 15 weeks old. More direct evidence still was sought from a study of reciprocal differences in an experiment in which Finnish Landrace and Merino sheep were crossed reciprocally. The breeds and their crosses were not, however, examined until more than 10 months old. The results (presented in paper 14) showed that the two pure breeds differed very markedly in plasma copper levels and showed that at this relatively late age 'carry-over' maternal effects were unimportant.

The crosses of Finnish Landrace with Merino, however, showed plasma copper levels halfway between those of their parent breeds - a result contrasting with the previous findings were crosses of different breeds had levels like those of the 'higher' parent. From the point of view of arriving at a generalisation about the inheritance of blood copper levels this new result was inconvenient and the reasons for it require further investigation. Direct breeding experiments to resolve the question are not, however, at present feasible and would take a considerable period of time. In the meantime it seemed appropriate to exploit additional information which could readily be obtained from these animals. The first studies of copper levels had been made on determinations in whole blood whilst later studies were made, mostly

for reasons of laboratory convenience, on blood plasma. It seemed plausible therefore that one of the contributory factors in the different behaviour of crossbreds relative to purebreds in these two experiments arose from some factor associated with whole blood, but not present in plasma.

An investigation was started therefore to associate copper concentrations with the genetically determined haemoglobin type in sheep. Haemoglobin type, which is a feature of the red cells, had already been under study by Dr. J.G. Hall in one of the flocks under consideration (the Blackface-Cheviot-Welsh one). Dr. Hall had found that the frequency of the haemoglobin type alleles differed among the breeds in this flock. Results of the new studies (paper No. 15) show a strong association of haemoglobin type with blood copper values in the flock in which the copper had been estimated in whole blood, and no association, or a non-significant association, in two other flocks in which plasma copper levels had been examined. Differences in copper concentrations between sheep of haemoglobin types A and B amounted to more than 40% of the fitted flock mean in mid-winter when average copper levels were low. This is far greater than other reported associations with haemoglobin type such as those with the concentration of some other red cell constituents which, in general, do not exceed about 5%.

Differences in copper levels of whole blood attributable to haemoglobin type were observed in this flock at various bleedings throughout the year and although such repeated observations on the same

animals are not independent of each other, the persistence of the effect precludes a simple seasonal explanation for the copper differences associated with haemoglobin type in one flock relative to the others. Within the flock in which the association was found some breed groups showed more pronounced differences in copper concentration between the haemoglobin types than did others, a fact which will assume greater prominence in the considerations which follow. As far as the results in paper No. 15 are concerned, the simplest hypothesis to fit the facts was that the copper difference attributable to haemoglobin type was associated with copper in the red cells. This then required direct experimental verification and the results are presented in paper 18. Copper levels were determined in whole blood, in cells and in plasma of sheep of two separate age groups drawn from later generations of the flock in which, originally, whole blood alone had been examined. The strong association previously found with haemoglobin type was again observed but the effect was primarily with copper in plasma. Again the effect was found at all seasons of the year and over a wide range of average plasma copper levels in the flock. This result must now be set alongside the absence of a corresponding association in the two other flocks already referred to which involved different breeds and different experiments. An association between copper concentrations in plasma and haemoglobin type might be expected to occur universally if it were attributable to a physiological effect or if the genes for haemoglobin type also directly affect copper levels (pleiotropy). Since there is no such universal association it seems more probably that effectively a single gene with a major effect on plasma copper levels exists which may be partially linked to the haemo-

globin type locus. In the Blackface-Cheviot-Welsh flock the presumed gene for 'high' copper appears to have become more often associated with the Hb B allele, or that for 'low' copper with Hb A. This might well have occurred initially by chance and have been perpetuated in this flock since it has been closed for several generations and deliberate, close inbreeding has been carried out. The fact that the differences between copper levels of A and B haemoglobin type sheep are greater in some breed groups (the Blackface and Welsh) than in others (the Cheviot) are then consistent with this hypothesis which depends both on the frequency of the 'high copper' allele in the population and on linkage.

To test the hypothesis of a 'copper gene' an experiment was recently started with the aim of selecting for plasma copper level independently of haemoglobin type. The results of the first year are given in paper 19 and show that when rams were selected for high and others for low plasma copper level (with a substantial difference between the two) within haemoglobin type, and mated to a random group of ewes, the progeny differed clearly in plasma copper level. This is consistent with the hypothesis proposed.

A particularly intriguing question posed by the evidence of genetic variation in the copper concentration of the blood and tissues of sheep concerns the mechanism whereby these differences arise. Another report based on current work (paper 20) shows clear breed differences in rate of repletion of copper as observed by changes in plasma copper levels following a period of depletion. The most plausible explanation implicates breed differences in the rate of absorption of

dietary copper, though there are other possibilities.

Other minerals in sheep and cattle

Evidence for breed differences in the concentration of calcium, magnesium and phosphorus in the blood plasma of sheep is presented in papers 6 and 11. Original estimates of heritability of mineral concentrations in the blood of cattle are given in a review paper (No. 12). This also includes an estimate of genetic variation in glucose concentration.

Whilst studies on these constituents, and the extension of the work from sheep to cattle, have not yet progressed far, they support the general thesis that genetic variation may be an important factor in controlling mineral requirements of ruminants. If glucose can be taken as a pointer (paper No. 12) the uptake or the utilisation of major nutrients may also show genetic variation.

Sections 2 and 3

In the present context the main purpose of the papers in these sections (papers 21-43) is to provide supporting evidence of the author's research contribution. Attention is, however, drawn to a number of points arising from these papers.

Experimental animal breeding studies (section 2)

A particular problem in livestock improvement is to differentiate between genetic and non-genetic factors influencing production. Farm effects and management practices, the effect of maternal environment, birth type and type of rearing, and factors involving disease are among non-genetic factors not only affecting performance of the animal subjected to them but also, at times, 'carried over' to the next generation. For example, lambs from large litters may themselves have a reduced reproductive performance because of an early restriction on their body size. Non-uniformity of treatment of different breeds or other genetic groups may then be wrongly interpreted, as demonstrated in paper 33 which shows that the performance of three breeds ranked differently when compared in a common environment than when each breed was in its own 'typical' environment. All the papers in this section are concerned with the apportionment of variation to genetic and non-genetic sources for the various traits considered.

Four of the papers (22, 23, 24 and 31) are concerned with aspects of tooth eruption or dental occlusion in cattle and sheep and provide evidence of genetic variation as well as demonstrating the

influence of other factors. Poor occlusion and unsound teeth are involved in poor performance and pre-mature culling of animals, particularly sheep under hill grazing conditions, and the results of these studies therefore have practical implications. In the light of the evidence of genetic variation in aspects of mineral metabolism obtained later and particularly of the genetic variation in calcium and phosphorus levels in plasma, it may be worth asking whether this is associated in any causative way with the genetic variation in skeletal and dental development which these four studies tentatively suggested.

Papers 25 and 26 report the results of an experiment designed to study the causes of differences in milk production among herds. Particularly before the impact of the selection programmes linked to the widespread use of artificial insemination in dairy cattle, herd performance was often popularly equated with genetic merit - particularly because environmental and management differences are not often readily definable (see paper 26). The experiment reported in these papers showed that when members of pairs of cattle twins, purchased by the Animal Breeding Research Organisation, were allocated as calves to farms with either a high or a low-yielding dairy herd, the members on the 'better' farms grew more rapidly than their twin sisters on the 'poorer' farms. Subsequently, the milk yield of the twins was close to that of other cows in the herds into which they were placed. This provided experimental support for the conclusion already drawn from population studies - to which the papers in section 3 of this submission had contributed - that most of the differences in milk yield between dairy herds were environmental and not

genetic in origin.

Most of the remaining papers in this section are based directly on an experiment with sheep involving breed comparisons, crossbreeding and inbreeding (papers 30, 35, 36, 37) or an offshoot from it (papers 27, 29, 32). They are concerned with a variety of traits including, growth, maternal performance, fleece characteristics and lamb survival. This experiment also provided the stimulus and basis for most of the studies on genetic aspects of mineral metabolism reported in section 1. In view of this work, the aspects concerned with genetic variation in lamb survival are especially relevant. There is tentative evidence for it in paper No. 30 and clearer evidence in paper 37. It also confirms the fact noted in paper No. 1 that crossbred sheep survive better than expected on the basis of mid-parental levels. Attention should also be drawn to paper No. 34 which reports results from a survey, initiated by the author to investigate breed variation in lamb mortality and lambing rate under commercial farm conditions. This work was undertaken as a consequence of the author's experimental findings on breed variation in lamb mortality in general and that due to swayback in particular. The study further supports the idea that the factors underlying the ability of lambs to survive, or their ability to resist disorder, are partly attributable to heredity.

Studies on cattle and sheep populations (section 3)

This section deals with operational research undertaken before experimental facilities had become available to the author. Most of the data used in the five papers (38-42) on cattle had been

previously used in a submission by the author for the Ph.D. degree at Edinburgh University in 1950, although extensions and re-analysis were included in the published papers. The study of sheep populations (paper 43) was started subsequently.

The studies were designed to show the structure and dynamics of breed organisation and how this affected the potential for genetic improvement of livestock.

Section 1

Studies on genetic aspects of mineral metabolism

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16. Wiener, G., Hayter, Susan, Field, A.C. and Macleod, N.S.M. 1974. Copper levels in liver and brain of dead lambs in relation to breed, age at death and cause of death. J. Comp. Path., 84, 27-28.

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20. Wiener, G. Breed differences in repletion of plasma copper concentrations following depletion (unpublished).

Section 2

Experimental animal breeding studies on various traits of cattle and sheep

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Section 3

Studies of cattle and sheep populations

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GENETIC AND OTHER FACTORS IN THE OCCURRENCE OF SWAYBACK IN SHEEP

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INTRODUCTION

Swayback has been reported as a source of loss among lambs in a number of countries and in sheep of different breeds (for references see Barlow, Purves, Butler and MacIntyre, 1960a). Clinical, pathological and certain biochemical aspects of the disease have been studied to a considerable extent and reported in the literature (Barlow, Purves, Butler and MacIntyre, 1960b). Evidence has now come to light that genetic factors influence the incidence of swayback and that there are also associations with other variables such as, for example, date of birth, the number of lambs per ewe and body size. The present paper presents some of this evidence for three flocks of sheep involving two farms and a period of years from 1952 to 1965. Apart from the incidence of swayback, the incidence of losses from other causes is also reported.

MATERIALS AND METHODS

Flock 1

Animals. The findings are derived from an experiment in which three breeds of sheep, Scottish Blackface, South Country Cheviot and Welsh Mountain, are being compared with each other and with crosses made between these breeds with respect to a large number of characteristics. Additionally, the comparisons are made at different levels of inbreeding of both purebreds and crossbreds. The flock consists of non-inbred (F_1 and F_2), 25 per cent. inbred (I_1), 37½ per cent. inbred (I_2) and 50 per cent. inbred (I_3) animals (but for 1964 see also below). All the experimental animals were born and bred on the farm and are the descendants of about 40 females and 6 males of each of the three pure breeds purchased as lambs in 1955.

Sheep of the F_1 class were produced by mating ewes of each of the three pure breeds with unrelated rams of these same three breeds, thus reproducing the three pure breeds and creating six types of crossbred. The F_2 class was produced from F_1 animals by mating together unrelated animals of the same pure breed or cross. The inbred classes were generated from parent × offspring matings, and occasional full sib matings, starting with animals of the F_1 or F_2 classes. The analysis pertains to the year 1964 when an outbreak of swayback occurred. The 418 lambs born alive in that year belonged to the F_2 class and to all the inbred classes. Thirteen of the inbred lambs, however, had inbreeding coefficients between 12·5 and 20 per cent., because a few ewes had to be mated to a less closely related ram than planned. The mothers of the lambs all belonged to the F_1, F_2 of I_1 class.

There were a few isolated cases of swayback in this flock in years preceding 1964—these are recorded separately from the main results. Ewes are kept until 5½ years old. They are mated so as to lamb for the first time at two years old and they have the opportunity to produce four lamb crops at yearly intervals. There is no culling for any characteristic associated with the performance of the animals.

In 1964 the non-inbred lambs (F_2) were born to 5-year-old ewes (mostly parity 4). The inbred lambs were born to 2-, 3- and 4-year-old ewes (parities 1, 2 and 3). Single-born lambs were reared as singles. Twins and the four sets of triplets born were reared either as twins or as singles. All lambs were reared by their dams except for two twin-born and two triplet-born lambs which were fostered, as singles, and three twin-born lambs which were bottle-fed.

Farm environment and management. The upland farm, Blythbank in Peeblesshire, comprises fields of sown pastures. The sheep stay out of doors all the year round, but hay and concentrates are provided as a supplement from early February. The ewe flock is run together as a single unit (an exception is described below) moving from field to field as grazing management requires. There is no separation by breed, age, type of offspring or rearing, e.g. single or twin. Ewes of all types are mated during the same period of time of about seven weeks. The lambs run with their mothers from birth—lambing starts in the second week of April—to weaning at 15 weeks of age but, for ease of management, the flock is divided during this time into three sub-groups according to the week of birth. The sub-groups are kept in separate fields providing similar grazing and they are moved from field to field at frequent intervals. The sub-groups are amalgamated after weaning.

Flock 2

Animals. These were 4-year-old Blackface and a few Blackface × Swaledale ewes which had been obtained several years previously at the age of about 18 months from nine different sources. Swayback occurred in 1964. At mating time in November 1963 the ewes were allocated so that each ram received an equal sample of ewes from each source. There were two rams of each of five breeds viz. Border Leicester, Clun Forest, Dorset Horn, Finnish Landrace and Merino. The ewes were left with the appropriate ram for 40 days, and thereafter turned out with a Cheviot ram whose offspring were excluded from the swayback analysis.

Farm environment and management. The farm Broughton Knowe in Peeblesshire is on exposed upland. For most of the year the sheep were carried on an area of open unimproved hill land, but mated in fields with sown pastures. Subsequently the ewes were returned to the hill where they were managed as one flock receiving some hay and concentrates from mid-February until early May. The ewes lambed on the hill starting in early April; those which produced and reared twins were transferred to the fields mentioned above until weaning in mid-August. No triplets were born. One twin was fostered as a single. All other lambs were reared by their dams. Blythbank hill, which was used for some sheep related to flock 2 at Broughton Knowe, represents an unimproved hill area at Blythbank—a part of the farm not used by flock 1.

Flock 3

Animals. Swayback occurred in 1952. In that year the flock consisted of Blackface ewes, from one to five years old, bred on the farm, The lambs were sired by eight rams, four Border Leicester, two pure Wiltshire and two Wiltshire-Blackface crosses. Females were mated to lamb for the first time at one year of age. Among the mates of the Border Leicester rams one female was one year old at lambing, the remaining being between two and five years old. One of the pure Wiltshire rams was mated to females of all ages. The other Wiltshire and the two Wiltshire × Blackface rams were mated only to the females lambing at one year old. The flock was dispersed in 1954.

Farm environment and management. The farm is the same as for flock 1, and the general management was similar. Except for mating time, all ewes were run continuously as a single flock. Apart from one set of triplets all the lambs were singles or twins. They were reared by their mothers except for eight twin lambs and one of the triplets which were fostered as singles and one single-born lamb which was bottle-fed.

Definition of Swayback

A total of 19 lambs showing symptoms of ataxia early in the lambing period were sent for pathological and biochemical examination and were diagnosed as having swayback. Thereafter, lambs showing ataxia in each flock and year were assumed to have swayback. The flocks were under the supervision of experimental officers. In flock 1, lambs were under general surveillance in the fields each day and under close observation and individual examination every three weeks from birth until the age of 18 weeks. In flocks 2 and 3 individual examination was less frequent.

Although a few cases of ataxia were observed in the first week of life of the lambs, the majority were noted after the third week. Not all these cases resulted in death. Deaths of lambs not showing ataxia occurred mostly in the first week. Such lambs were not as a rule autopsied, but the few that were had diseases other than swayback. It is possible, however, that the other deaths included a number of incipient swayback cases. The "real" incidence of swayback in the flocks studied may, therefore, have been greater or smaller than that reported, depending on the validity of the assumptions made for purposes of classification.

Although there is some year-to-year variation in the incidence of lamb losses in these flocks the incidence was appreciably higher than normal in 1952 and 1964 when particular outbreaks of swayback occurred. In these years the incidence of other losses alone, excluding the cases of ataxia, was within the normal range of total losses in "non-swayback" years.

RESULTS

Breed and Sire Effects

Tables 1, 2 and 3 show the incidence of swayback and other losses in each of the three flocks sub-divided by breed and, for two flocks, by sire within breed. In flock 1 different breeds and crosses of ewes were mated with rams of the same breeds and crosses, whereas in flocks 2 and 3 only the breed of ram varied.

TABLE 1

INCIDENCE OF SWAYBACK AND OF OTHER LOSSES UP TO 18 ~~YEARS~~ WEEKS

Flock 1 (1964). According to breed in three flocks of sheep and also according to sire in two of the flocks. Dams and sires of lambs of the same breed or cross

Breed or cross of lamb*	*No. lambs*		*Percentage of no. born alive*	
	Born alive	*Stillborn*	*Swayback*	*"Other" losses*
Scottish Blackface	48	1	39·6	35·4
Cheviot	35	1	11·4	22·2
Welsh Mountain	56	1	0·0	17·9
Blackface × Cheviot	92	2	20·6	13·0
Blackface × Welsh	106	0	15·1	12·3
Cheviot × Welsh	81	4	4·9	21·0
All breeds	418	9	14·8	18·4

* The crossbred lambs are from matings of crossbred ewes with crossbred rams of the same type (e.g. (B×C)♀ × (C×B)♂).

Flock 1. Differences due breed were large and highly significant ($P<0{\cdot}001$). The highest incidence, nearly 40 per cent., was in pure Scottish Blackface and contrasted markedly with the absence of swayback among the pure Welsh Mountain lambs. No further sub-division by sires was made for this flock because the average number of offspring per sire was only about three. For each crossbred

group the incidence of swayback was not significantly different from the average of the incidence for the two appropriate pure breeds. If data from purebreds and crossbreds are pooled, the incidence of swayback associated with Blackface, Cheviot and Welsh "blood" was 24·9 per cent., 12·7 per cent. and 6·7 per cent., respectively, and for "other losses" 20·2 per cent., 18·5 per cent. and 16·7 per cent., respectively. The incidence of losses ascribed to non-swayback causes ranked, among the three pure breeds, in the same order as the incidence of swayback. It seems unlikely, therefore, that "other losses" would have masked the "real" incidence of swayback to a greater extent in those breeds which showed little swayback than in those which showed a lot.

Swayback cases had occurred in the same flock in earlier years as follows: six in 1958, one purebred Blackface and five first crosses with Blackface; one purebred Blackface, single-born, in 1962, and both members of one pair of purebred Blackface twins in 1963. In total, these additional cases represent 72 per cent.

TABLE 2

INCIDENCE OF SWAYBACK AND OF OTHER LOSSES UP TO 18 ~~YEARS~~ WEEKS

Flock 2 (1964). Dams of lambs predominantly of Blackface breed plus a few Blackface × Swaledale, sires of lambs as shown

Breed of sire	*Sire*	*No. lambs*		*Percentage of no. born alive*			
		Born alive	*Stillborn*	*Swayback*		*"Other" losses*	
				Sire	*Sire's breed*	*Sire*	*Sire's breed*
Border Leicester	(i)	28	0	10·7	6.0	14·3	10·0
	(ii)	22	0	0·0		4·5	
Clun Forest	(iii)	24	2	16·7	26·0	4·7	2·0
	(iv)	26	0	34·6		0·0	
Dorset Horn	(v)	29	0	3·4	6·9	0·0	3·4
	(vi)	29	0	10·3		6·9	
Finnish Landrace	(vii)	25	0	8·0	15·1	0·0	1·9
	(viii)	28	0	21·4		3·6	
Merino	(ix)	26	0	3·8	5·6	7·7	8·3
	(x)	10	0	10·0		10·0	
All sires		247	2		12·1		4·9

Blackface blood whereas the average proportion of Blackface blood among all lambs born in these years was about 30 per cent.

Flock 2. Differences in the incidence of swayback due to breed of sire were significant ($P<0·01$), but largely on account of the greater incidence among the lambs with fathers of the Clun Forest breed (Table 2). The individual sires differed very significantly ($P<0·001$) from each other in the incidence of swayback among their offspring. Most of the total variation in the incidence of swayback was accounted for by these sire differences and when variation due to sires was removed from the total, breed differences were no longer significant. There were no significant differences in swayback incidence due to the original source from which the mothers of the lambs had been derived.

Each of the ten rams was mated to between four and seven ewes additional to those which remained in flock 2 and whose offspring are recorded in Table 2.

These additional ewes, 59 in all, were moved in December 1963—after completion of mating—to the Blythbank hill. Among the 83 lambs born at this new location there was only one case of swayback—the offspring of a Finnish Landrace ram (No. VIII).

Ninety of the female lambs born in flock 2 in 1964 which had been free from swayback symptoms were moved in September of the same year to Blythbank and were mated to purebred Welsh Mountain rams. Six cases of swayback were confirmed among the 105 lambs born alive in 1965, three of them with a Merino grand-sire (27 per cent. of the lambs in this class), two with a Finnish Landrace grand-sire (6 per cent.) and one with a Border Leicester grand-sire (5·5 per cent.). Neither the Clun Forest nor the Dorset Horn grand-sires were implicated (Table 2).

Flock 3. The difference in swayback incidence between the offspring of Border Leicester sires on the one hand and Wiltshire or Wiltshire × Blackface sires on the other was highly significant ($P<0·001$), but within each of these two

TABLE 3

INCIDENCE OF SWAYBACK AND OF OTHER LOSSES UP TO 18 ~~YEARS~~ WEEKS

Flock 3 (1952). Dams of lambs of Blackface breed, sires of lambs as shown

Breed of sire	*Sire*	*No. lambs*		*Percentage of no. born alive*			
		Born alive	*Stillborn*	*Swayback*		*"Other" losses*	
				Sire	*Sire's breed*	*Sire*	*Sire's breed*
Border Leicester	a	17*	0	35·3	25·0	5·9	14·6
	b	5*	0	0·0		20·0	
	c	13*	0	15·4		23·1	
	d	13**	0	30·8		15·3	
Wiltshire	e	26†	2	0·0	0·0	11·5	13·0
	f	20‡	2	0·0		15·0	
Wiltshire × Blackface	g	10‡	0	0·0	0·0	10·0	25·0
	h	14‡	1	0·0		35·7	
All sires		118	5		10·2		16·1

*All lambs born to females aged from 2 to 5 years old.
** 12 lambs born to females aged from 2 to 5 years old, 1 to a 1-year-old female.
† 20 lambs born to females aged from 2 to 5 years old, 6 to 1-year-old females.
‡ All lambs born to 1-year-old females.

groups individual sires did not differ significantly from each other. Only one of the rams in the Wiltshire group (ram e) was mated, as were the Border Leicester, to females lambing at 2 years old and over (see Materials and Methods and footnote to Table 3). When the breed comparison was restricted to the Border Leicester and this one Wiltshire ram, the difference in swayback incidence among their offspring was still significant ($P<0·02$).

Breeding System

In Table 4, lambs of flock 1 are classified according to whether they were purebred or crossbred, outbred, i.e. 0 per cent. inbred, or inbred. The four classes did not differ significantly in the incidence of swayback, but they differed very markedly ($P<0·001$) in the incidence of other losses. On average crossbred

lambs were at an advantage over purebred ones and outbred lambs over inbred ones in avoiding deaths other than swayback, but not in respect of avoiding swayback itself. The genetic implications of this will be discussed later. Outbred lambs were born to 5-year-old ewes, inbred lambs to ewes of 2, 3, or 4 years old. This disparity has not affected the validity of the above findings (see below).

Age of Ewe

Flock 1. There was no statistically significant difference in the incidence of swayback among inbred lambs from the three ages of ewe. Ages corresponded in the majority of cases to the appropriate parities, e.g. 2-year-old = parity 1. Percentage incidences of swayback and of other losses (in parentheses) were as follows: from 2-year-old, 18·7 (24·0); 3-year-old, 12·8 (23·0); 4-year-old, 12·9 (21·1). For swayback none of these differed significantly from the incidence of 16·7 per cent. among the outbred lambs from 5-year-old ewes, but for other losses, as inferred from the last section, this age class had a lower incidence— 5·9 per cent.— presumably not primarily on account of age but on account of breeding.

TABLE 4

INCIDENCE OF SWAYBACK AND OTHER LOSSES EXCLUDING STILLBIRTHS

In relation to breeding system and pure versus crossbred stock (flock 1 only)

	Outbred			*Inbred*			*Unweighted average*	
	No.	*Swayback* %	*Other losses* %	*No.*	*Swayback* %	*Other losses* %	*Swayback* %	*Other losses* %
Purebred	26	15·4	11·5	113	16·8	28·3	16·1	19·9
Crossbred	75	17·3	4·0	204	12·7	19·1	15·0	11·6
Unweighted average	—	16·4	7·8	—	14·8	23·7	15·6	15·7

Flock 3. Among the lambs with Border Leicester sires there was no significant difference attributable to age of dam. The number of swayback cases and the appropriate total number of lambs, in parentheses, were as follows: 1-year-old, 0 (1); 2-year-old, 3 (9); 3-year-old, 3 (8); 4-year-old, 5 (14); 5-year-old, 1 (16).

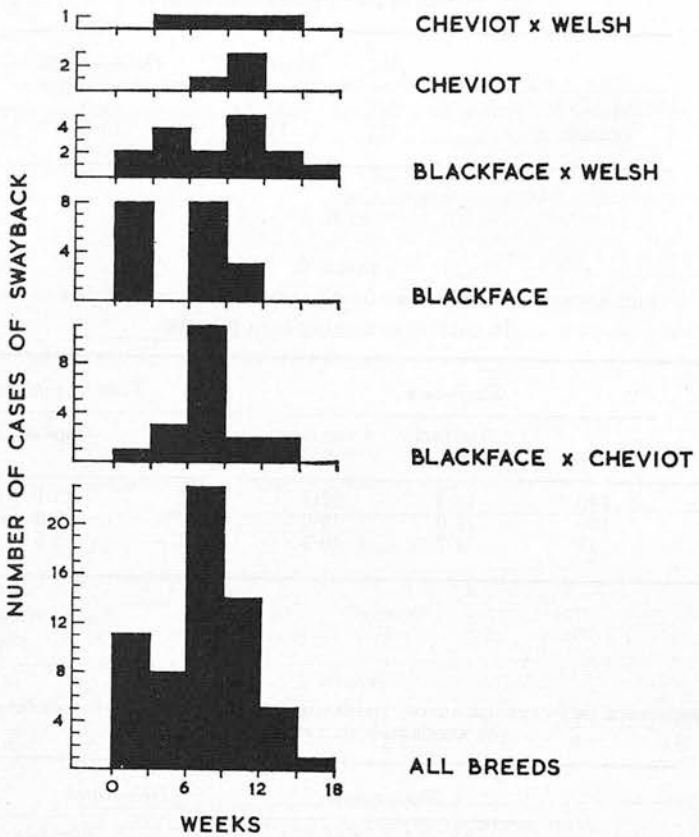
Age at which Ataxia was First Noted and Age at Death

Flock 1. Four Blackface lambs died from swayback within two days of birth, the next at 22 days old, and the first lamb of another breed died at 26 days old. Fourteen lambs with swayback symptoms survived weaning at 15 weeks old and were then slaughtered. Fig. 1 shows, for each three-week period from birth, the time when ataxia was first noticed. There was a tendency for the Blackface lambs to display swayback symptoms somewhat sooner than the other breeds and this was not only by virtue of the four early deaths. The frequency distributions for the six breed types, shown in Fig. 1, just differ significantly ($P = 0{\cdot}05$).

Flock 2. Seven of the thirty affected lambs died before weaning without any breed or sire disproportionately implicated. The age when ataxia was first seen was not recorded.

Flock 3. The twelve affected lambs died between days 2 and 62 after birth. There were no obvious differences attributable to sire. The age when ataxia was first seen was not recorded.

Fig. 1.



Frequency distributions showing, for each breed and cross in flock 1, except the Welsh breed where no swayback occurred, the number of lambs for which swayback symptoms were first recorded in each 3-weekly period from birth.

Birth Type and Rearing

Sex. There was no significant difference between male and female lambs in the proportion with swayback symptoms or in the proportion of other losses. This applied in each of the flocks separately and for the combined data shown in Table 5.

Number of lambs born per ewe. Table 6 shows the incidence of swayback and of other losses among single-born and twin-born lambs in each of the three flocks.

In flocks 1 and 3 there was a slight, non-significant tendency for twin-born lambs to have the higher incidence of swayback. In flock 2 the tendency was the opposite and was statistically significant ($P<0.01$), but the ewes rearing twins in this flock were run on better land than those rearing singles. In all three flocks other losses were slightly, but not significantly, higher among single than among twin-born lambs.

TABLE 5

INCIDENCE OF SWAYBACK AND OTHER LOSSES EXCLUDING STILLBIRTHS

In relation to sex (3 flocks combined)

	No.	*Swayback %*	*Other losses %*
Male	371	12·7	14·0
Female	412	13·3	13·6

TABLE 6

INCIDENCE OF SWAYBACK AND OTHER LOSSES EXCLUDING STILLBIRTHS

In relation to number born per ewe

	Single-born			*Twin (or triplet)-born*		
	No.	*Swayback %*	*Other losses %*	*No.*	*Swayback %*	*Other losses %*
Flock 1	140	14·3	22·9	278	15·1	16·2
Flock 2	100	17·0	5·0	147	8·8	4·8
Flock 3	37	2·7	18·9	81	13·6	14·8

TABLE 7

INCIDENCE OF SWAYBACK AMONG TWINS SURVIVING MORE THAN TWO WEEKS OF AGE ACCORDING TO TYPE OF REARING

	Single-reared		*Twin-reared*	
	No.	*Swayback %*	*No.*	*Swayback %*
Flock 1	33	18·2	198	16·2
Flock 2	8	62·5	132	3·8
Flock 3	22	18·2	51	7·8

Rearing of twins. Twins were classified according to how they were being reared, i.e. as single or as twin, at two weeks old. Swayback cases occurring prior to that time have therefore been excluded from Table 7. There was a tendency for twins reared as singles to have a higher incidence of swayback than twins reared as twins, but only in flock 2, where ewes rearing twins had different grazing from ewes rearing singles, was the difference significant ($P<0.001$).

Association between twins. Twin pairs were classified according to whether both members of each pair, one, or neither showed swayback symptoms. The number of pairs where both or neither member showed swayback symptoms was greatly in excess of the numbers expected on the assumption that the members of a twin pair were independent of each other in respect of their chances of showing the symptoms ($P<0{\cdot}001$). This occurred in each flock. Among the 190 twin pairs (Table 8) where no lambs were lost from causes other than swayback, 18 pairs, compared with an expected 3·4, had both members showing swayback symptoms, 15 pairs, expected 44·1, had one member with swayback and 157 pairs, expected 142·5, were apparently free from swayback. The same general pattern occurred

TABLE 8

ASSOCIATION BETWEEN MEMBERS OF TWIN PAIRS AND THEIR FATE

Three flocks combined. Number of pairs of twins observed in each class

No. of pair members dying from "other" causes	*No. of pair members with swayback symptoms**		
	Both	*One*	*Neither*
Both	—	—	10
One	—	13	37
Neither	18	15	157

*For "expected" numbers see text.

TABLE 9

INCIDENCE OF SWAYBACK AND OTHER LOSSES IN RELATION TO WEEK OF BIRTH

	Flock 1			*Flock 2*			*Flock 3*		
Lambs born in week	*No. born alive*	*Swayback %*	*Other losses %*	*No. born alive*	*Swayback %*	*Other losses %*	*No. born alive*	*Swayback %*	*Other losses %*
1	191	22·0	15·2	75	18·7	8·0	41	12·2	14·6
2	108	10·2	20·4*	68	5·9	2·9	49	4·1	14·3
3	33	9·1	12·1	79	11·4	3·8	20	25·0	20·0
4	34	17·6	17·6	14	14·3	7·1	8	0·0	25·0
5–8	52	0·0	30·8	11	9·1	0·0	—	—	—

*15·7% if six lambs which were accidentally poisoned are excluded (see text).

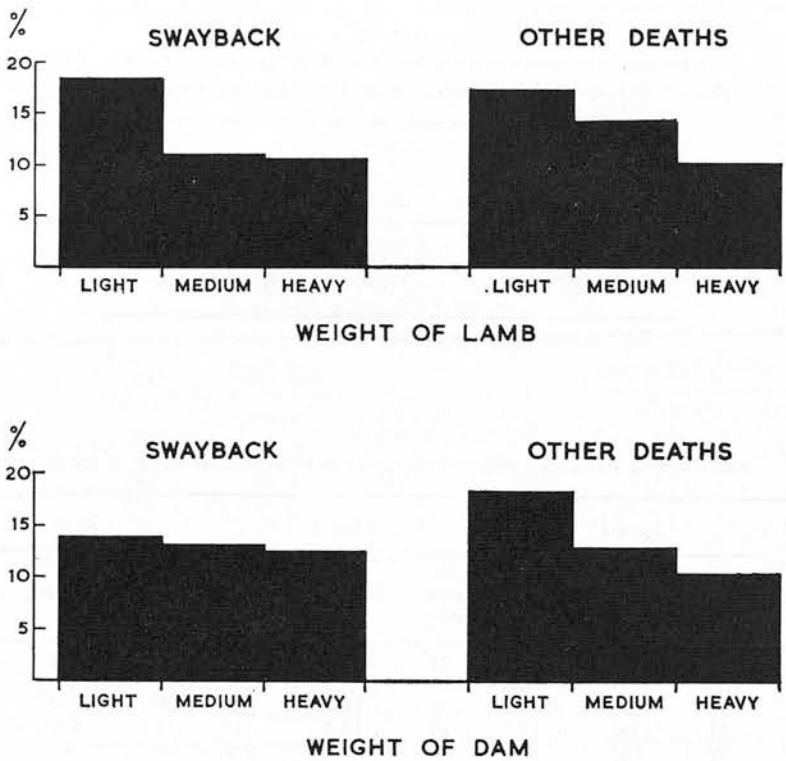
for "other losses", but the deviations from expectation were much smaller than in the case of swayback and not significant for flocks 1 and 3, but significant ($P<0{\cdot}01$) in aggregate. There were 204 twin pairs (Table 8) where no swayback occurred. In 10 of these pairs, expected 4·0, both twins died, in 37 pairs, expected 49·1, one twin died and 157 pairs, expected 150·9, survived intact.

Week of Birth

In flocks 1 and 2 the incidence of swayback was highest for lambs born in the first week of the lambing period (Table 9). Differences in the incidence of swayback among the different weeks were highly significant ($P<0.001$) for flock 1,

but not for the other two flocks. By contrast, there was a tendency for other losses to be higher later in the lambing season, but not in flock 2. Differences between weeks in respect of these other losses were significant ($P<0{\cdot}05$) only on the combined data from the three flocks. In flock 1, a group of eight lambs born in the second week of lambing were experimentally dosed with $CuSO_4$ in order to prevent the onset of delayed swayback. Six of the eight lambs died within 48 hours and no further lambs were so treated. These six lambs might legitimately be excluded from the "other losses" shown in Table 9.

Fig. 2.



The proportion of lambs with swayback and the proportion lost for other reasons among lambs grouped into three classes according to birth weight and weight of dam (data from 3 flocks combined).

Body Weight

To ascertain if there was a connection between the incidence of swayback and body size, the lambs were ranked according to their own birth weights and according to the weights of their dams at mating. Three groups with equal numbers were formed containing respectively the lightest, middle-weight and heaviest weights. The division was made separately for each flock within litter size class and within breed for flock 1, within sire for flock 2 and within sires' breed for flock 3. The numbers of swayback cases and other losses were noted for each weight group and totalled over sub-classes. The combined results from the three

flocks are shown in Fig. 2. The lightest lambs had significantly more swayback than the middle-weight or heavy ones ($P<0{\cdot}01$), but the dam's weight appeared to have had very little effect on swayback incidence. Other losses were significantly but not surprisingly different among the different weight groups of lambs ($P<0{\cdot}05$); more interestingly they differed significantly among the weight groups of dams ($P<0{\cdot}05$).

It is apparent, therefore, that, because of their unequal representation among the birth-weight classes, swayback lambs and lambs lost for other reasons must, on average, be lighter in weight at birth than lambs which survived to weaning. When the lambs in appropriate sub-groups were classified according to their fate it was found that among single-born lambs there was a tendency for swayback lambs to be, on average, lighter in weight at birth than lambs which survived, but those lost for other reasons were, on average, lighter still. For twin-born lambs differences between the three fate categories of lamb were not obvious. Within the breed classes of flock 1 single-born lambs which suffered swayback also had less heavy mothers than those lambs which survived; the lambs that were lost for other reasons had the dams of lightest average weight. For twin-born lambs in flock 1 and for all lambs in the other two flocks an association between fate of lamb and weight of mother was not obvious.

DISCUSSION

The sporadic occurrence of swayback over a period of years in the three flocks studied makes it necessary to assume predisposing environmental circumstances. This point has been discussed by, for example, Allcroft (1952) and Barlow *et al.* (1960a). Supporting evidence in the present study comes from the contrast of a twelve per cent. incidence of swayback in flock 2 at Broughton Knowe and a one per cent. incidence among a genetically similar group at Blythbank in the same year. Clearly, however, this study shows that once the predisposing circumstances are present there are considerable and significant differences in the incidence of swayback between genetically different groups, i.e. between different breeds and between different sire families.

The implication of some measure of genetic control for differences in the incidence of swayback arises not only from the presence of the differences between the breeds and sire families in the three flocks but from the fact that the incidences among the crossbred lambs in flock 1 were intermediate between those of the appropriate purebred types of lamb and not significantly different from the mid-parental values. This fact, and the similarity of incidence among outbred and inbred lambs derived from the same base populations suggests that much of the genetic variation in susceptibility to swayback, or resistance to swayback, is additive in nature. This contrasts strongly with the evidence presented here for heterosis in respect of the general ability to survive. In practical terms, the chances of a lamb surviving the usual hazards in its early weeks of life seem to be good if it is a non-inbred of crossbred foundation and rather bad if an inbred of purebred stock. The chances of getting swayback seem to be little affected by these considerations. It also follows from this evidence that it should be possible to select against susceptibility to swayback, although the likely measure of success cannot be estimated from the present data since they are not suitable

for the calculation of heritabilities. One may speculate that one reason why natural selection has not already created the same genetic situation in respect of swayback as of deaths from other causes is that whereas natural selection operates with varying intensity every year and under all conditions on the composite character of survival, swayback is subject to natural selection only in the occasional years and under the particular circumstances which predispose to its occurrence. It may be also that the situations are not strictly comparable in the present instance since the majority of swayback cases arose from 3 weeks onward which is relatively late whilst the majority of other losses were deaths in the first week of life.

The evidence that if one member of a twin pair gets swayback the co-twin will get it also is extremely strong. The maternal effect on members of the twin pair is clearly implicated although there is no means in these data of differentiating between the relative importance of the genetic contribution of the mother to her offspring and the effects of the maternal environment. Maternal blood copper levels are known to be associated with the occurrence of swayback of lambs (Allcroft, Clegg and Uvarov, 1959; Butler and Barlow, 1963) and thus represent one possible pathway of the maternal effect.

Breed differences in the incidence of swayback also appear to be associated with differences in blood copper levels of the ewes (Wiener and Field, 1966). Ewes from flock 1 were bled nine months after the swayback outbreak among their lambs and significant differences were found between the breeds in average blood copper levels. The association with previous swayback incidence was close since, for example, Blackface ewes had the lowest average blood copper levels and their lambs the highest incidence of swayback—and vice versa for the Welsh breed.

Among the non-genetic factors associated with the incidence of swayback, week of birth had the strongest association although it is not clear why the first group to be born should have had the highest incidence and the second group, a week later, almost the least. Further evidence from blood copper analyses in flock 1 at the subsequent lambing, made in 1965 one year after the outbreak of swayback (Wiener and Field, unpublished), points to possible differences in blood copper levels associated with the week of birth of the lambs.

The first attempt to associate body weight with the incidence of swayback among lambs has shown no consistent association with ewes' weight, but has suggested a link with the birth weights of lambs. No clue is contained in this relationship as to which might be cause and which effect.

CONCLUSIONS

Data on the incidence of swayback have been presented from three grassland flocks of experimental sheep for the period 1952 to 1965. Among the 971 lambs 111 were recorded as having swayback, mostly of a delayed type. Several breeds and crosses were involved as well as inbred and outbred sheep. The aim of the management of each experimental flock was to ensure that genetic and environmental differences were not confounded.

In the first flock, 40 per cent. of Scottish Blackface, 11 per cent. of Cheviot and none of the Welsh Mountain lambs had swayback symptoms. Crossbred lambs were intermediate in swayback incidence between the appropriate purebred types.

Inbreds did not differ from outbreds. In the second flock, two rams of each of five diverse breeds had been mated to ewes of the Blackface breed. Sires differed very significantly from each other in the incidence of swayback among their offspring varying between 0 per cent. and 35 per cent. In the third flock, the incidence of swayback was significantly associated with breed of sire.

The age at which swayback symptoms were first noted appeared to be associated with breed.

There was a very strong association in the chances of having swayback between the members of twin pairs.

Sex of lamb had no effect on swayback incidence. The number of lambs born and the number reared per ewe were significantly associated with swayback incidence in only the one flock where twins and singles were reared apart. The incidence of swayback differed significantly with the week of birth. More swayback cases arose among lambs light in birth weight than among heavier ones. There was no consistent difference in incidence of swayback for lambs from light, medium or heavy weight classes of ewe. Preliminary evidence suggests that the weight relationships with swayback may differ for single and twin lambs.

The occurrence of swayback has been studied alongside the occurrence of death from other causes. Genetic implications of the findings are discussed.

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Blood Copper-levels in Sheep in Relation to Genetic Factors, Parity and Previous Swayback History

BLOOD copper-levels are known to be associated with the incidence of swayback in lambs (see Barlow *et al.*)[1]. A sample of fifty-five ewes was bled some 6 weeks prior to lambing and almost a year after a 15 per cent incidence of swayback had occurred among the lambs in the flock from which these ewes were drawn. The flock consists of three breeds (Scottish Blackface, South Country Cheviot and Welsh Mountain) and the crosses between these breeds. The ewes belong to two breeding classes, outbred (F_2) and 25 per cent inbred (I_1), and to four parities. The choice of animals for bleeding took account of these subdivisions within this flock and of swayback history of the lambs born to ewes of parity 2 and more in 1964. Blood copper values were estimated by the method of Butler and Newman[2].

The blood copper values (obtained by least squares) for the effects of breed and differences due to inbreeding, parity (in-lamb for first time versus later parities), swayback history and cross-breeding, are shown in Table 1. Breed had an apparent effect on total variation in blood copper ($0{\cdot}1 > P > 0{\cdot}05$), although not all the six breed types differed significantly from each other. On average, Blackfaces had the lowest blood copper value. Heterosis was suggested by the crosses having on average higher values than the average of the purebreds ($0{\cdot}1 > P > 0{\cdot}05$). The difference between inbreds and outbreds was not significant. Most clearly, ewes which nearly a year ago

Table 1. BLOOD COPPER VALUES (μG/100 ML. WHOLE BLOOD) FOR SIX BREED TYPES OF EWE AND DIFFERENCES DUE TO CROSS-BREEDING, INBREEDING, PARITY AND SWAYBACK HISTORY

Class	Copper value*	*S.E.*
Blackface	27·79	4·80
Cheviot	35·35	4·78
Welsh	40·50	4·70
Cheviot–Welsh	43·15	4·83
Blackface–Welsh	37·89	4·67
Blackface–Cheviot	40·75	4·67
Cross-bred mean–purebred mean†	6·05	3·35
I_1–F_2	−3·63	3·32
Deviation, from later parity ewes with no previous swayback lambs, of		
First parity ewes	−10·08	4·26
Later parity ewes with previous swayback lambs	−15·68	3·98

* The breed effects shown refer to the F_2 class and to the later parity with no previous swayback lambs. The average of the six fitted breed values (37·57) may be compared with the actual average of 28·55 for the blood copper values determined for the 55 ewes.

† Difference derived from the fitted breed values.

produced lambs with swayback had much lower blood copper values than contemporaries which had previously had normal lambs ($P < 0{\cdot}001$). Females in-lamb for the first time had significantly lower values than ewes which had lambed previously ($P < 0{\cdot}05$).

For about 6 weeks prior to bleeding, the ewes, which ran together as one grassland flock, had access to a mineral lick containing 718 p.p.m. copper. It is possible, therefore, that sheep may have ingested different quantities of mineral, which could complicate interpretation of the results. However, the special management circumstances of the experimental flock are such that there was no segregation of the flock by breed or by the other subdivisions in the analysis. In spite of the access to a mineral lick containing copper, only two of the fifty-five sheep had blood copper values greater than the 60 μg/100 ml. whole blood, which has been accepted as a 'normal' level in the literature (for references see Barlow *et al.*[1]).

It has recently been found[3] in the same flock that the incidence of swayback in lambs in 1964 was clearly associated with breed and breed cross. The mean blood copper values of the three pure breeds ranked inversely to the percentage of lambs with swayback among these breeds in the previous year. The overall correlation between the present blood copper levels of the six breed types of ewe and the percentile incidence of swayback among the lambs of the same six breed types in the same flock a year ago was $-0{\cdot}82$ ($P < 0{\cdot}05$). The genetic implications of these findings merit further investigation in relation to the swayback syndrome.

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3

COPPER CONCENTRATIONS IN THE LIVER AND BLOOD OF SHEEP OF DIFFERENT BREEDS IN RELATION TO SWAYBACK HISTORY

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INTRODUCTION

In a flock of sheep comprising the Scottish Blackface, South Country Cheviot and Welsh Mountain breeds and the crosses between them Wiener and Field (1966) found that breed affected the level of copper in the blood. An outbreak of swayback among the lambs in the same flock in the previous year had shown that the incidence varied with breed (Wiener, 1966), and that this incidence was closely associated with the mean copper concentration in the blood of the six breed classes of sheep when bled nine months after the swayback outbreak (Wiener and Field, 1966).

The present investigation was carried out to ascertain whether the concentration of copper in the liver of sheep would also show genetic differences and to investigate the relationship between liver and blood copper concentrations in each breed.

MATERIALS AND METHODS

Sixty-eight sheep were bled one day prior to slaughter in October 1966 to estimate the blood copper levels by the method of Brown and Hemingway (1962). At slaughter a sample of liver from the left lobe was taken from each sheep, freeze dried, wet ashed (Butler and Newman, 1965) and the copper concentration in the ash solution determined directly by atomic absorption (AA2 Hilger Watts Ltd.).

The sheep comprised the Scottish Blackface, South Country Cheviot and Welsh Mountain breeds and the crosses (F_2) between them. Both the purebred and the crossbred sheep were represented by two breeding classes, outbred and inbred. Among the purebreds there were 15 outbred and 17 inbred and among the crossbreds 15 outbred and 21 inbred. The inbreeding coefficient was 25 per cent. except for one crossbred animal with a coefficient of 37·5 per cent. These sheep were drawn from the same flock as the 55 bled in February 1965 and featured in the previous report by Wiener and Field (1966), but only 10 of the sheep appear in both samples. The sheep belonged to two age classes, 18 months ("young") and $4\frac{1}{2}$ to $6\frac{1}{2}$ years ("old"). The 54 old sheep, but not the 14 young ones, had produced lambs in 1966. Among the old sheep, 5 had produced lambs with swayback symptoms in the spring of 1964, i.e. $2\frac{1}{2}$ years previously.

All the sheep and their progenitors have been on the same farm since 1955. The sheep between the ages of about 4 months and 18 months were kept as a separate group from the older ones, but in similar, often adjacent, fields. The sheep were moved from field to field at frequent intervals. Supplementary feeds of hay and concentrates during snow and prior to lambing were available to the whole flock and no abstentions from feeding by particular groups of sheep have ever been observed.

In February, 1965 and again in February, 1966 the ewes, but not the young, non-pregnant females, were injected with 50 mg. copper as copper calcium edetate* to reduce the chances of swayback among the lambs which had occurred in 1964. No cases of swayback were recorded in the two years in question.

Statistical analysis took the form of least-squares estimates of the effects of breed, age, previous swayback history and inbreeding on copper concentrations. The covariance of copper concentrations in liver and in blood was added as a further constant. Constants were fitted in stages so that the reduction in the sum of squares attributable to the various effects could be calculated.

RESULTS

General Description

The liver and blood copper values are shown in Fig. 1. In terms of the

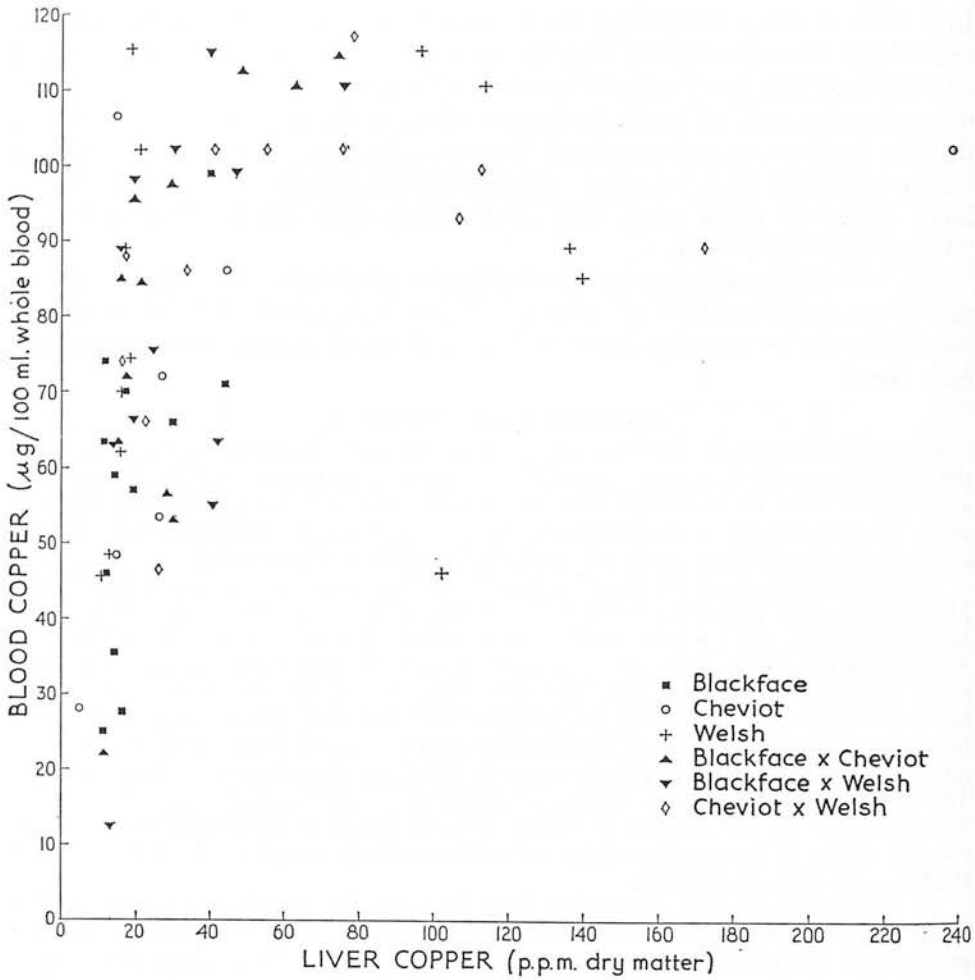

Fig. 1. Concentrations of copper in the blood and in the liver of 68 female sheep of six breeds maintained as a single flock.

*'Coprin', Glaxo Laboratories.

coefficient of variation, liver values were three times as variable as blood values. The relationship between blood and liver copper concentrations is seen to be curvilinear. With one exception, the sheep with concentrations of copper in their livers in excess of 50 p.p.m. had blood copper levels above 80 μg./100 ml., but animals with high concentrations of copper in their blood did not necessarily have high concentrations in their livers. The values for the concentration of copper in the livers from the Welsh Mountain sheep showed a bimodal distribution. Five had levels above 95 p.p.m. and 8 had levels below 21 p.p.m. More data would be needed to determine whether this is a genuine feature of the breed. Although there was considerable overlap among the breeds, some breed differences were also apparent.

TABLE 1

COPPER CONCENTRATIONS OF LIVER (P.P.M. OF DM) AND OF WHOLE BLOOD (μg./100 ml.)
Six breeds of female sheep and differences due to cross-breeding, inbreeding, age and previous swayback history (fitted values obtained by least squares)

		All 68 sheep			
		Copper in			
*Class**	*No. of animals*	*liver*		*blood*	
		Fitted value	*SE*	*Fitted value*	*SE*
Blackface	12	14·3	13·8	59·8	7·6
Cheviot	7	44·7	17·0	66·8	9·4
Welsh	13	49·7	13·1	75·7	7·2
Blackface x Cheviot	12	26·2	14·3	80·8	7·9
Blackface x Welsh	12	23·2	13·9	78·6	7·7
Cheviot x Welsh	12	54·9	13·6	84·4	7·5
Crossbred-purebred†		−1·5	10·5	13·8	5·8
Inbred-outbred		17·7	11·7	5·1	6·5
Deviation from old females with no previous swayback lambs of:					
(a) young, non-parous females		−12·9	14·8	8·0	6·5
(b) old females with previous swayback lambs		−5·4	20·7	−35·4	11·4
Overall mean		41·9	5·3	76·8	3·2
Sum of squares due to fitting constants as per cent of total		16·7		31·2	
regression MS (8df) / residual MS (59df)		1·48		3·37	

*The breed values shown refer to old females of the outbred class with no history of swayback among their lambs in 1964.

†Difference of means of the fitted breed values.

Sources of Variation

The results of fitting constants are shown in Table 1. The total variation in liver copper removed by the constants was not statistically significant. The value for the Blackface breed stood out as being lower than the values of the other breeds and, on its own, removed a significant ($P < 0{\cdot}01$), though small, proportion of the total variation. It should be noted also that the three breed groups involving the Blackface breed showed markedly lower values on average than the three others ($P < 0{\cdot}02$). Conversely, the average of the breed groups in-

volving the Cheviot was higher and the average involving the Welsh breed higher still. The respective differences were not, however, statistically significant. Crossbred sheep had, on average, no higher a liver copper concentration than the average of the pure breeds. Females which had given birth to lambs with swayback in 1964 did not have significantly less copper in their liver dry matter than females which had normal lambs in 1964.

The results for the copper concentration in the blood are also shown in Table 1 and agree with the results from similar sheep bled at a different time of year previously reported by Wiener and Field (1966). Here, a significant proportion ($P < 0{\cdot}01$) of the total variation was removed by fitting the constants. Variation due to breeds in general was not significant, but that due to the Blackface breed in particular was significant. The pure breeds again ranked Blackface, Cheviot, Welsh in order of rising copper values as reported formerly and the crosses again had significantly more copper ($P < 0{\cdot}05$) in their blood than the purebred sheep. Females which had produced swayback lambs in 1964 had a markedly lower concentration of copper in their blood than "normal" contemporaries and this was a highly significant factor in the total variation ($P < 0{\cdot}01$).

Liver-Blood Relationships

Regression. When the regression of liver copper-level on blood copper level was added as a further variable in the analysis of liver copper concentration, the amount of variation removed by fitting constants (30·4 per cent.) became highly significant ($P < 0{\cdot}01$), the regression of liver level on blood level alone accounting for a large part of this. The analogous procedure for blood copper showed that the regression on liver copper accounted for a further highly significant proportion (11·3 per cent.; $P < 0{\cdot}01$) of the total variation. The average regression coefficients, as fitted constants, were:

$$b_{\text{liver. blood}} = 0{\cdot}73 \pm 0{\cdot}21 \ [(\text{p.p.m. liver DM})/(\mu\text{g./100 ml. blood})]$$
$$b_{\text{blood. liver}} = 0{\cdot}22 \pm 0{\cdot}067 \ [(\mu\text{g./100 ml. blood})/(\text{p.p.m. liver DM})].$$

The regression coefficients for blood on liver copper levels for the different breeds and crosses, calculated for animals which had not produced swayback lambs, ranged from $0{\cdot}14 \pm 0{\cdot}14$ for the Welsh breed to $0{\cdot}94 \pm 0{\cdot}43$ for the Blackface, but the breed differences were not statistically significant. However, the average coefficient for the three groups involving the Blackface breed ($0{\cdot}92 \pm 0{\cdot}20$) was significantly higher ($P < 0{\cdot}001$) than the average coefficient involving the other three breeds ($0{\cdot}17 \pm 0{\cdot}07$). Differences among regression coefficients of liver on blood copper levels for the different breeds were not significant.

Because the relationship of blood and liver copper levels was not linear (see Fig. 1), a better description of the data is obtained by relating copper concentration in the blood to the reciprocal of the concentration in the liver. When added as a further constant in the analysis of blood copper the reciprocal of liver copper concentration accounted for a further 31·0 per cent., compared with 11·3 per

cent. for the actual liver values, of the total variation. The average regression coefficients when all animals were included were:

$b_{1/\text{liver. blood}} = -0{\cdot}000756 \pm 0{\cdot}000137$ [(1/p.p.m. liver DM)/(μg./100 ml. blood)]

$b_{\text{blood. 1/liver}} = -449{\cdot}0 \pm 83{\cdot}2$ [(μg./100 ml. blood)/(1/p.p.m. liver DM)]

or, $-0{\cdot}000694 \pm 0{\cdot}000109$ and $-597{\cdot}1 \pm 95{\cdot}7$ respectively when two of the 68 animals were excluded because of the apparently odd relationship of liver and blood copper levels recorded for these two animals (see Fig. 1: a Welsh ewe with a liver copper level above 100 p.p.m. and a blood level below 50 μg./100 ml., and a Cheviot ewe with an estimated liver copper concentration of only 5 p.p.m.). The regression coefficients involving blood copper level and the reciprocal of the copper level in the liver did not differ significantly among the different breeds or between the Blackface and its crosses on the one hand and the non-Blackface types on the other.

TABLE 2

CORRELATIONS BETWEEN THE CONCENTRATION OF COPPER IN THE BLOOD AND THE CONCENTRATION, OR THE RECIPROCAL OF THE CONCENTRATION, IN THE LIVER

	Degrees of freedom in brackets		
	Total correlation	*Correlation of fitted values**	*Residual correlation*
Blood with liver			
All 68 females	0·43 (66)	0·53 (8)	0·41 (58)
66 females†	0·45 (64)	0·50 (8)	0·45 (56)
Blood with 1/liver			
All 68 females	−0·61 (66)	−0·73 (8)	−0·58 (58)
66 females†	−0·65 (64)	−0·71 (8)	−0·64 (56)

*Fitted for the effects of the classes shown in Table 1.
†Two females excluded because of their odd values (see text).

Correlations. Table 2 shows correlations between copper concentration, or its reciprocal, in the liver and the concentration in the blood. Three correlations are shown, total correlations, correlations of the fitted values and residual correlations. The total and residual correlations were statistically significant. The correlations of fitted values were based on a smaller number of degrees of freedom and only those involving the reciprocal of the liver copper concentrations reached significance. The correlation of fitted values indicates to what extent the factors chosen as constants have a common effect on blood and liver copper concentrations. The correlations suggest that whereas about half the variation attributable to breed and other factors is common to blood and liver copper concentration, only about one-third of the variation within breeds is common to both.

Table 2 also reflects the better statistical relationship of blood copper values with the reciprocal of the liver values than with the liver values as recorded. Consideration of the partial correlations, not shown in Table 2, when blood, liver and 1/liver values were analysed together, showed that holding liver values constant caused only a slight lowering of the correlation between blood and 1/liver copper concentrations, but holding the 1/liver values constant virtually

eliminated the correlation between blood and liver copper concentration. This re-emphasizes the non-linear relationship between blood and liver copper concentrations. A statistical disadvantage in the use of the reciprocal of liver copper concentration arises because at low concentrations of copper, i.e. large reciprocals, errors in determining the copper values can affect the reciprocal markedly, whilst at high concentrations errors affect the reciprocal very little. The importance of this will depend on the magnitude of the errors involved in the determination of copper concentration.

DISCUSSION

Nine months and 21 months prior to the experiment the ewes had been injected with 50 mg. copper as a prophylaxis against swayback. Since the amount of copper injected per unit liveweight of the sheep was not constant and the breeds differed in average weight, it is possible that a carry-over effect could be partly responsible for the breed differences in copper concentrations. For blood copper level this appears to be unlikely, however, because the evidence of Butler and Barlow (1963) suggests that such carry-over effects are eliminated from the blood in a much shorter time than the present interval between injection and bleeding. Moreover, the breeds ranked in virtually the same order in respect of their blood copper level in the present study and in the earlier one (Wiener and Field, 1966) which preceded copper injections. For liver copper level there is no equivalent evidence. It should be noted, however, that if there were a carry-over effect from the copper dosage it could not have been directly related to the weight of the sheep because the Blackface and Cheviot, for example, differed markedly in average liver copper concentrations, but were virtually the same in average liveweight.

Although no cases of swayback were recorded in 1965 and 1966, the five ewes in the present sample which had produced swayback lambs in 1964 had, as a class, a lower level of copper in the blood than ewes which had produced normal lambs. The level in the liver for this class was not, however, significantly different from the average level of the other ewes.

Genetic effects on the concentration of copper in the liver were seen in the significant contribution of the Blackface breed to the total variation and in the significantly lower concentrations of copper in the livers of Blackface females and their crosses on the one hand and of non-Blackface (Cheviot, Welsh, and Cheviot × Welsh) females on the other. It is possible that the extremely high variability of copper levels in the liver may have masked other differences found for blood levels.

The relationship between concentrations of copper in the blood and in the liver were explained by common factors such as breed in only fairly small part in relation to the total variation. However, the copper concentrations for the three pure breeds ranked in the same order of magnitude (Blackface $<$ Cheviot $<$ Welsh) for both blood and liver and this is supported by other, as yet unpublished, data from the same flock. The effect of crossing the breeds appeared, however, to have a heterotic effect. It raised the copper level in the blood to approximately the level in the parental breed with the higher value, as also found in a previous study (Wiener and Field, 1966). Concentrations of copper in the

livers of the crossbred sheep were more nearly intermediate between the levels of the two contributing pure breeds. The average of the crossbreeds was not different from the average of the purebreds. The inference may be drawn from this that the availability of copper to the blood was not entirely dependent on the level in the liver and that the balance maintained in the blood may be independently influenced by genetic factors. More data, however, would be needed to substantiate this hypothesis. Some support comes from the fact that ewes which had produced swayback lambs more than two years previously had lower concentrations of copper in their blood, but not apparently in their livers.

Breed differences in copper concentrations, to the extent that they apply to both the blood and the liver, could operate by altering the ability of the animal to absorb dietary copper and by modifying the endogenous excretion of copper in the faeces and the excretion in the urine.

Further studies of the genetic aspects of copper metabolism are in progress.

SUMMARY

The concentrations of copper in the blood and in the liver were determined for 68 female sheep of two age classes drawn from a genetically diversified grassland breeding flock. The flock comprised three breeds, Scottish Blackface, Cheviot and Welsh Mountain, and their crosses. Some sheep were inbred and some outbred, and they included a few which had produced swayback lambs two years previously. Constants were fitted for these various factors. They accounted for a significant proportion (31 per cent.) of the total variation in copper concentration in blood, but not in liver (17 per cent.). The copper concentrations ranked in the same order of magnitude for both blood and liver (Blackface $<$ Cheviot $<$ Welsh), but the crossbreds showed heterosis in blood copper concentration, but not in liver. The Blackface and its crosses had a significantly lower copper concentration in the liver than the three non-Blackface groups. Ewes which had formerly produced swayback lambs had a significantly lower blood copper level, but the level in the liver was average.

There was a curvilinear relationship between blood and liver copper concentration. Expressed as the correlation between blood copper concentration and the reciprocal of the copper concentration in the liver, its coefficient was $r = -0{\cdot}6$. The regressions of blood on liver values and vice versa were not significantly different for the various breeds except those for sheep involving the Blackface breed ($^{b}_{\text{blood. liver}} = 0{\cdot}92 \pm 0{\cdot}20$) and those excluding the Blackface ($^{b}_{\text{blood. liver}} = 0{\cdot}17 \pm 0{\cdot}07$).

Copper concentrations in the liver was three times as variable, in terms of the coefficient of variation, as in the blood and this may contribute to the lesser significance of genetic variation in copper concentration in the liver than in the blood.

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4

The concentration of minerals in the blood of genetically diverse groups of sheep

I. Copper concentration at different seasons in Blackface, Cheviot, Welsh Mountain and crossbred sheep at pasture

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SUMMARY

The concentration of copper in the blood of more than 300 sheep of a grassland flock was determined on each of five occasions between May 1965 and June 1966. Six breed classes, Scottish Blackface, Cheviot and Welsh Mountain, and the three crosses among these breeds, were involved.

Breeds differed significantly in blood copper concentration with the Blackface having consistently the lowest and the Welsh the highest values. Crossbred sheep showed marked heterosis. Their levels were mostly at or near to the concentration of the parental breed with the higher value. Within breeds there was a positive regression of blood copper level on live weight of ewe.

Ewes which had produced lambs affected by swayback in 1964 had lower levels of copper in their blood than ewes which had produced normal lambs. The difference was significant and most marked in winter.

Ewes which were barren had, subsequently, higher blood copper concentrations than ewes with lambs. Ewes with single lambs had on average slightly higher levels than those with twins (but not significantly so), however, the effect differed among the breeds. Blood copper levels differed significantly on most occasions with the week in which ewes lambed in relation to the date of bleeding. Age of ewe had significant effects on copper concentration only at one bleeding (January 1966).

There was an indication that classes low in copper concentration, notably Blackfaces and mothers of swayback lambs, showed a relatively steeper decline in copper levels during the winter than did other sheep.

INTRODUCTION

Particular interest in the 'mineral status' of sheep has followed, in recent years, on the intensification of husbandry through feeding, housing and the reclamation and improvement of hill pastures. Specific metabolic disorders are associated with excess, deficiency or imbalance of minerals in the diet and with variation in the absorption, excretion and retention of minerals by the animals, while effects short of clinical disease may well contribute to suboptimal performance of animals (for reviews see Blaxter, 1959, 1960, 1961).

Studies of the mineral status of ruminants in relation to requirements have revealed remarkably high variation among individual animals (see, for example, Agricultural Research Council, 1965). There is little or no indication, however, whether any of the variability can be attributed to hereditary differences except in relation to a few specific disorders and to the well established single gene effect on the concentration of potassium in the red blood

cells of sheep first shown by Evans & King (1955).

The present series of studies is concerned with variation in the concentration of minerals in the blood of sheep in relation to genetic factors and to sources of variation common to groups of sheep in a flock, e.g. their lambing performance, age, seasonal factors, and so on.

The present paper deals with the concentration of copper in the whole blood of the sheep at different seasons in a grassland flock comprising the Scottish Blackface, Cheviot and Welsh Mountain breeds and their crosses. Preliminary evidence from this flock had shown the importance of breed differences in blood copper concentration and also the importance of swayback among lambs as a source of variation in the blood copper concentration of their mothers in a later year (Wiener & Field, 1966).

MATERIALS AND METHODS

Blood sampling. Sheep were bled on five occasions.

1. May or June 1965, in groups 6 weeks after lambing ($\pm 3\frac{1}{2}$ days). Barren ewes were bled on the same date as ewes lambing in week 3 of the lambing period.

2. 19 or 20 October 1965.

3. 31 January 1966—one day prior to copper injection (see below).

4. May or June 1966 in groups 6 weeks after lambing ($\pm 3\frac{1}{2}$ days) (barren ewes with lambing group 3 as before).

5. 7 June 1966—all sheep (including barren) irrespective of lambing date.

The numbers of sheep are shown in Table 1.

Copper estimation. The method of Brown & Hemingway (1962) was used.

Animals. The findings are derived from an experiment in which sheep of the Scottish Blackface, South Country Cheviot and Welsh Mountain breeds are being compared with each other and with crosses (F_2) made between these breeds with respect to a large number of characteristics. Additionally comparisons are being made at various levels of inbreeding of both pure breds and cross-breds (0, 25, $37\frac{1}{2}$ and 50 %). The animals were born and bred on the farm and are the descendants of about forty females and six males of each of the three pure breeds purchased as lambs in 1955 and described both in terms of their performance and management by Wiener (1967).

Females in this flock are normally discarded at $5\frac{1}{2}$ years old, thus not all the mothers of lambs born in 1964 have survived to later years. A few also died, but no culling took place for reasons associated with the performance or health of the sheep. Numbers in excess of requirements were culled at random within breeding classes, usually before the sheep reach 18 months old.

In October 1965 the normal disposal of old ewes

Table 1. *The effects of breed (at equal live weights of ewe and including the adjusted flock mean), live weight of ewe and swayback history on the concentration of copper in the whole blood (μg/100 ml.) on four occasions*

	Effects and standard errors							
	Summer 1965*		October 1965†		January 1966†		June 1966†	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Number of sheep	306		351		347		307	
Breeds								
Blackface	79·4	3·3§	50·3	4·3	37·0	4·1	58·2	4·2
Cheviot	88·6	3·2	65·6	3·9	46·9	3·7	79·5	3·9
Welsh	99·2	3·3	97·8	4·0	66·8	3·8	98·2	4·1
Blackface × Cheviot	88·9	2·6	66·5	3·2	55·7	3·0	79·7	3·3
Blackface × Welsh	101·8	2·3	83·2	2·8	61·0	2·6	87·7	2·9
Cheviot × Welsh	104·6	2·5	85·3	2·9	60·9	2·7	95·0	2·9
Cross-bred–pure bred‡	9·4	2·4	7·1	3·0	9·0	2·8	8·8	3·0
Live weight of ewe within class (units of Cu per 10 lb wt)	0·7	0·7	2·6	0·8	1·7	0·9	2·4	1·0
Deviation of ewes with swayback lambs in 1964 from ewes with normal lambs	−4·8	4·5	−14·3	6·5	−17·4	6·1	−5·1	6·3

* Ewes bled in groups 6 weeks after lambing.
† Ewes bled on one day.
‡ Difference between adjusted flock means.
§ Breed S.E.'s apply to deviations from flock average.

was modified by the retention of a few of each breed to produce extra lambs to compensate for a 15% loss of lambs due to swayback in 1964 (Wiener, 1966). Non-parous females entering the breeding flock for the first time at 18 months old were bled in October 1965 and subsequently. Five age classes were thus included in the experiment.

Farm environment and flock management. The farm, Blythbank, Peeblesshire lies at an elevation of 800–1000 ft. The sheep were run in fields of sown pastures. The females from the age of weaning (15 weeks old) until the age of 18 months were kept as a separate group from the older ewes which in turn were managed, except between lambing and weaning, as a single group throughout their life. The sheep stayed out of doors all year round, but hay and concentrates were provided as supplements from early February until lambing or shortly afterwards, the amounts depending on the season. The food was available to the whole flock and abstentions by particular groups of sheep have not been observed.

All ewes were individually penned with a ram when they came into oestrus. Mating took place over the same period of about 8 weeks from the beginning of November. For convenience the ewes with their lambs were divided into three subgroups solely according to week of birth of the lambs and kept that way until weaning. Thereafter the subgroups were again amalgamated. The three subgroups were formed by combining ewes giving birth to lambs in: (*a*) weeks 1, 4 and 7 of the lambing period, (*b*) weeks 2, 5 and 8, and (*c*) 3, 6 and 9 with the addition of the barren ewes. The subgroups were kept in separate but similar fields and were frequently moved between fields.

In February 1965 and again in February 1966 the ewes, but not the young, unmated females, were injected with 50 mg copper (as copper calcium edetate, 'Coprin', Glaxo Laboratories). No cases of swayback were recorded in the two years in question.

Statistical analysis. This consisted of fitting a linear model with parameters representing the effects of breed, live weight of ewe, swayback history, inbreeding, various aspects of lambing performance, date of lambing in relation to bleeding, and age of ewe. The final model is represented by the parameters shown in the tables. A larger number of parameters, relevant to the sheep in each of the 2 years covered by the bleedings, was fitted to each set of data in the first place. Interactions of breed with age of ewe and breed with number of lambs born were also fitted. Factors (i.e. groups of parameters representing, for instance, the breeds) were eliminated from further consideration if both singly and in combination with other factors they were found to have a high probability of being due to chance. The final model, which was applied to the data of all five bleedings represented those factors which were found to have statistically significant effects on at least one occasion. In the case of the data pertaining to 31 January 1966, aspects of lambing performance in 1965 and in 1966 both merited inclusion in the analysis. Choice was made then on the basis of the degree of statistical significance of the effects. This principle was also adopted in the choice of live weight (January 1965, September 1965 or January 1966) to relate to each set of copper data.

The sums of squares attributable to the various factors were calculated by excluding each in turn from the final model. The significance of the effects were then deduced.

The adjusted flock mean, in relation to which some of the results are presented, is expressed in terms of sheep which are 'averaged' for breed, inbreeding class, week of lambing, number of lambs born, age, and live weight within class; furthermore, it relates to ewes which produced lambs (non-barren), which were born prior to 1964, and which, if they lambed in 1964, produced normal (non-swayback) lambs.

RESULTS

For convenience, the effects of related parameters have been grouped in the tables. The values shown are the estimates when all other parameters in the analysis were held constant.

The tables show the results of only four of the five blood sampling occasions. The results from the bleeding of groups 6 weeks after lambing in 1966 have been excluded for brevity of presentation. The conclusions to be drawn from them are essentially the same as those from the bleeding on 7 June, with the important exception of effects associated with week of lambing in relation to week of bleeding which will be referred to later. Variability in blood copper concentration was higher (mean square = 765 (μg/100 ml.)^2) for 7 June data than for the other (mean square = 592 (μg/100 ml.)^2), but the factors considered accounted for 30·4% of the total variation in the former case and only 20·6% in the latter.

In general the results show a seasonal pattern of change in blood copper concentration with higher values in summer than in winter. Variability also changed but in the opposite direction. Thus the coefficient of variation was greatest in winter. The coefficients of variation (%) were 23, 39, 48 and about 31 in summer 1965, October 1965, January 1966 and summer 1966 respectively.

Breed. Breed was a highly significant source of variation in blood copper level at each bleeding. Table 1 shows the breed effects (at equal live weights of ewe) with the adjusted flock mean included. Among the pure bred sheep, Blackfaces had clearly the lowest value at all four seasons and Welsh the

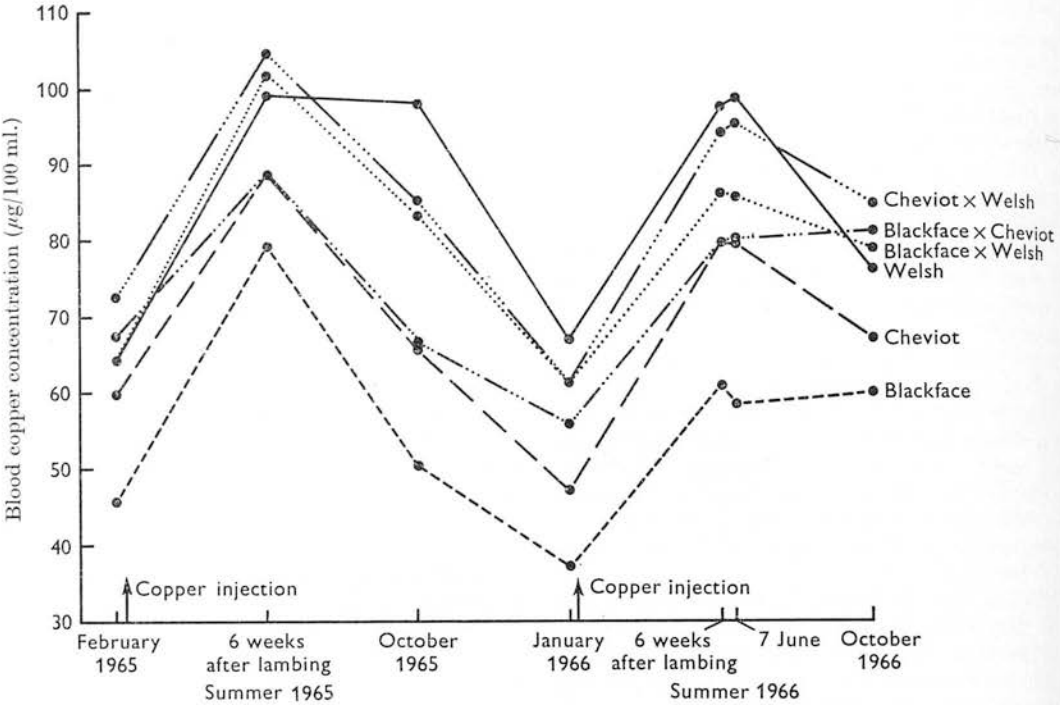

Fig. 1. Concentrations of copper in the blood of six breed classes of sheep on seven occasions when other factors of variation are held constant. The adjusted mean of the flock is included in the breed values. (First and last points on the graph are based on samples of ewes drawn from the flock; fewer factors were included in the statistical analysis of their copper data, see text.)

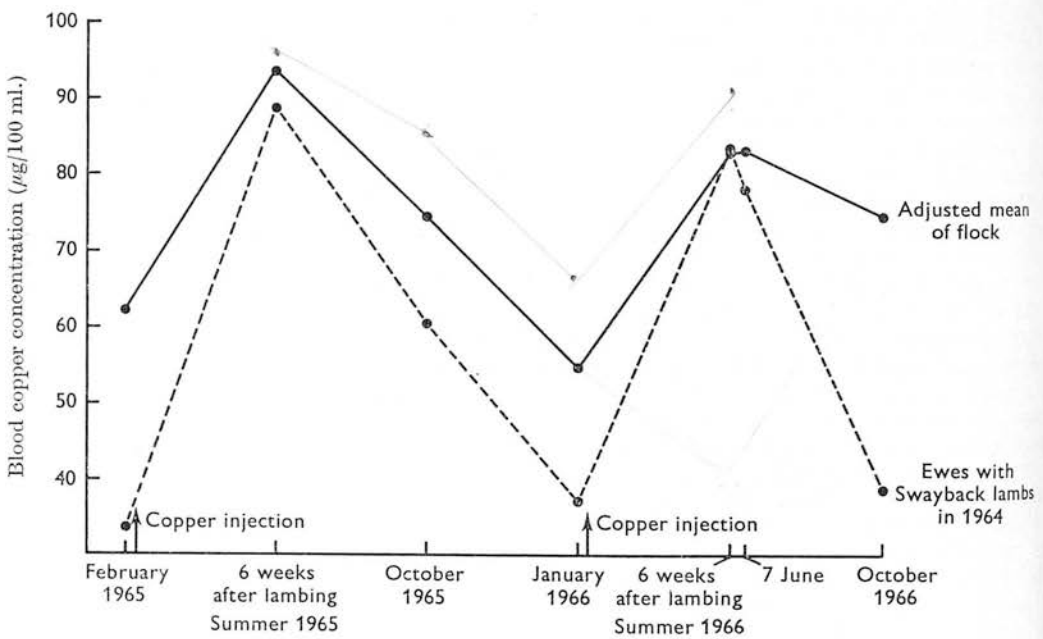

Fig. 2. Concentrations of copper in the blood of adult female sheep which produced swayback lambs in 1964, in relation to the adjusted mean of the flock, at seven subsequent occasions.

highest. Cross-breeding had the effect of raising the level of copper in the blood significantly above the mid-parental level, and mostly to or near to the level of the parental breed with the higher concentration of copper. In the face of this marked heterotic effect the most apparent genetic contribution of the separate breeds to the cross-bred sheep was to set an upper limit to the level of copper in the blood.

The results for breed effects have been extended in the time scale of Fig. 1 to include additional data from two stratified samples of ewes from the same flock, fifty-five ewes in February 1965 and sixty-eight in October 1966 (Wiener & Field, 1966, 1968). For February 1965, results from copper determinations by the method of Brown & Hemingway (1962) have been substituted for those previously published. Comparison of the precise breed values from the sample data and the new data is not strictly valid because of different models used in the analyses. Within these limitations imposed by sample size, however, Fig. 1 shows clearly the seasonal cycle in copper values, the unchanged ranking of the three pure breeds and the relative advantage of the cross-bred sheep. The fitted breed values for sheep bled 6 weeks after lambing (with a mean date of 26 May) are also shown in Fig. 1. These were on average slightly higher than the values for 7 June.

Live weight of ewe. Within classes, the association of live weight of ewe with blood copper level was found to be positive. Thus the heavier the ewe the higher its concentration of copper in the blood. The regression coefficients are shown in Table 1; not all are statistically significant.

The positive relationship within classes contrasts with a negative one among the breeds. Thus at the extremes the lightest of the breeds, the Welsh, had among the highest average copper levels and the Blackface, with the lowest average copper level was among the heaviest of the six breed classes.

Swayback history. Ewes which had produced lambs with swayback in 1964 had lower blood copper levels at all bleedings, than those which had produced normal lambs in that year. Table 1 shows the effects to have been greater at the October and February bleedings than in the summer of 1965 and 1966. In the summer the differences were not significant but in the winter they were. Figure 2 extends the information, as before, by the inclusion of data from earlier and later bleedings. These further demonstrate the more extreme seasonal changes in blood copper concentrations of sheep known to have produced lambs affected by swayback compared with those which produced normal lambs.

Only twenty ewes with a swayback history remained in the flock by the summer of 1966. This seemed too small a number to subdivide further in order to study the effects of the various parameters separately for this group. Unadjusted averages suggest, however, that among the ewes with a swayback history the breed differences are of the same order of magnitude as among 'normal' ewes. This is particularly relevant to October 1965 and February 1966 when ewes with a swayback history differed, on average, most markedly from the rest.

Inbreeding. The sheep were classified according to the degree of inbreeding viz. 0, 25, 37½ and 50 % representing 0, 1, 2, or 3 generations of offspring × younger parent or full sib matings. Degree of

Table 2. *The effects of number of lambs at birth on the concentration of copper in the whole blood (µg/100 ml.) on four occasions*

	Effects and standard errors							
	Summer 1965*		October 1965*		January 1966*		June 1966*	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Barren ewes as a deviation from ewes with lambs	2·8	4·2	13·3	5·6	12·4	5·3	11·5	5·3
Ewes with single lambs as deviation from breed average† for:								
Blackface	1·1	3·5	3·6	5·1	2·3	5·0	4·3	4·0
Cheviot	−1·6	4·1	1·2	5·9	−1·8	5·5	−0·5	4·5
Welsh	−1·9	3·2	−2·0	4·5	−2·7	4·2	2·4	4·3
Blackface × Cheviot	−2·4	2·8	−6·1	4·1	−5·3	3·9	2·3	3·6
Blackface × Welsh	−4·5	2·5	−3·1	3·4	−1·0	3·2	−1·1	3·1
Cheviot × Welsh	−5·1	2·8	9·2	3·8	3·3	3·6	−0·1	3·3

* See Table 1.

† Deviations for ewes with twin or triplet lambs at birth take the same values with the opposite sign.

inbreeding was found to be a significant source of variation in blood copper concentration only in the two sets of data for the summer of 1966 ($P < 0.01$). Then the non-inbred sheep were found to have lower copper concentrations than the inbred ones, a trend which was also just discernible at the earlier bleedings. Non-inbred sheep were 1, 4, 5, and 12 μg copper/100 ml. whole blood, below the average on the four occasions shown in Table 1.

Lambing performance. Ewes which did not lamb in 1965 had significantly higher blood copper levels in October 1965 and on 31 January 1966. The effect on blood copper concentration in the summer of 1965 was in the same direction but not significant. Barrenness in 1966 significantly affected blood copper concentration of ewes bled on 7 June 1966. The effects are shown in Table 2. For copper concentration on 31 January 1966, barrenness in 1966 had no discernible effect.

By and large, ewes with single lambs had slightly, but not significantly, higher blood copper levels than ewes with twins or triplets at birth. There was, however, an interaction of breed with number of lambs at birth too large to be ignored as a source of variation but short of statistical significance. The direction of the effect of the interaction is interesting. It reinforced the disadvantage of twins on the level of blood copper in the case of the Blackface breed, which had a relatively low level of copper already, and lessened the disadvantage of twins in the case of the Welsh breed and most of the cross-bred types. Results from the Cheviot–Welsh cross-bred sheep were markedly inconsistent. The combined effect of lamb number and interaction are shown in Table 2.

Lambing group. Blood copper levels, in all sets of data except that of October 1965, differed significantly ($P < 0.05$) with the week in which ewes gave birth to their lambs in relation to the date on which they were bled. The interpretation of the effects varies according to whether the ewes were bled 6 weeks after lambing (summers 1965 and 1966) or on a fixed date (October 1965, 31 January 1966, 7 June 1966). Major components of the former are the increasing intervals between the date of copper administration (in February) and the date of bleeding, and week-to-week variations. A major component of variation when bleeding on a fixed date is the length of lactation (changing interval from lambing). In the latter case the general effect was for ewes that lambed early in the season to have had lower copper values than those which lambed later. In the case of the bleeding 6 weeks after lambing, the groups bled first had the higher values. The lambing period extended over about 9 weeks but in respect of 1965 the data from later groups were amalgamated prior to analysis. For 1966 the effects were calculated separately for each week but later ones were averaged for presentation in Table 3.

Data for February 1966 represents a special case in as much as first analyses had shown that both the week of lambing in the previous year and the week of lambing in the following spring (representing the stage of pregnancy at the time of bleeding) ought to be included in the analysis. In the final analysis the carry-over effect on blood copper from the previous lambing season (shown in Table 3) was statistically the more significant ($P < 0.05$). The effects of the current pregnancy ($P < 0.1$) showed that the two groups in the most advanced stages of pregnancy (about 10–12 weeks pregnant) had lower copper levels than the other sheep. However, among the groups less advanced in pregnancy (from about 3 to 10 weeks pregnant) there was considerable variation.

Age of ewe. This contributed significantly to variation in blood copper concentration only in the

Table 3. *The effects of week of lambing in relation to date of bleeding on the concentration of copper in the whole blood (μg/100 ml.) on five occasions*

	Effects and standard errors									
	Relative to lambing in 1965				Relative to lambing in 1966					
	Ewes bled 6 weeks after lambing Summer		Ewes bled on 1 day October		Ewes bled on 1 day				Ewes bled 6 weeks after lambing Summer	
					January		June			
Week of lambing	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
1	4·7	2·1	−4·2	3·1	−2·1	2·9	−17·7	3·6	3·0	3·4
2	2·2	1·9	−2·5	2·7	−3·7	2·6	1·0	3·3	7·2	3·1
3	−1·2	2·3	−1·2	3·3	−4·3	3·2	6·9	3·7	0·1	3·3
4 and later*	−5·7	2·8	7·9	3·4	10·1	3·2	2·6	1·7	−2·6	1·6

* Data from later lambing groups pooled prior to analysis for first three occasions. For the last two bleedings in 1966 the effects were calculated for each week separately but the later ones were averaged.

Table 4. *The effects of age of ewe on the concentration of copper in the whole blood (μg/100 ml.) on four occasions*

	Effects and standard errors							
	Summer 1965*		October 1965*		January 1966*		June 1966*	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Ewes born in 1964 as a deviation from ewes born earlier	—	—	−9·1	6·1	−19·8	5·8	−2·1	3·9
Deviation of ewes born in different years (before 1964) from their average								
Born 1963	3·7	2·7	−0·6	3·2	−9·8	3·0	−7·2	3·1
1962	−1·5	2·2	0·3	3·1	−1·6	2·9	0·5	3·0
1961	−2·0	2·1	0·2	2·8	4·9	2·6	3·5	2·8
1960	−0·1	2·4	0·0	4·2	6·5	4·0	3·2	4·2

* See Table 1.

data from 31 January 1966, when young sheep, pregnant for the first time, had markedly less copper in their blood than older sheep, but within the group of older sheep copper level also increased with advancing age (Table 4).

DISCUSSION

The two pre-eminent features of the results are the contributions of breed and of swayback history to the variation in the concentration of copper in the blood of sheep.

Breed differences, often large and always statistically significant, were seen at all seasons of the year. A consequence of the copper injection given to the sheep each February, and for the first time in 1965, might have been to eliminate or reduce the breed effects. Butler & Barlow (1963) have suggested that copper injection reduced individual variation in copper levels. Our evidence is consistent with this, at any rate as a short-term consequence. Equally, however, these findings could be a seasonal occurrence unrelated to copper injections.

The range of breed differences was also smaller in the summer, in spite of higher mean levels of copper, than in the winter. This again might be associated with the copper injection since the amount injected was not constant per unit live weight of the sheep, and the breeds differed in average weight. However, as reported in relation to copper in the liver (Wiener & Field, 1968), the Blackface and the Cheviot sheep were of very similar body weight, but differed markedly in copper concentration. Moreover, the within-breed association of live weight and blood copper level was found to be positive whilst a negative association might have been expected had the amount of copper injected per unit of live weight been a major determinant of the variation in blood copper levels. Butler & Barlow (1963) have shown that the effects of copper injection are unlikely to be detectable in the blood for much longer than 3 to 6 months. Following such an injection our sheep were not bled for between 3 and 5 months. Evidence from the same flock before any injection (Wiener & Field, 1966) showed a similar picture of breed differences (see Fig. 1).

The importance of genetic factors demonstrated by the pure breeds is emphasized by the copper values of the cross-bred sheep which were consistently higher than mid-parental values and usually at, or close to, the value of the parental breed with the higher concentration of copper. Non-additive genetic variation thus appears to play a part. The inbred sheep had either the same blood copper concentrations as the non-inbred sheep or slightly higher concentrations. This absence of inbreeding depression contrasts with the marked heterosis from breed crosses. Further analyses and further data would be needed to choose among several possible explanations. These include the possibility that the three breeds differ markedly in the frequencies of the genes associated with blood copper levels, but that non-allelic interactions are responsible for the cross-bred advantage. Or the possibility, not exclusive of others, that lambs low in copper survive less well if they are also inbred than if they are non-inbred.

In consequence of the positive association within classes of blood copper level with live weight, breed differences in copper levels were greater at equal weights of ewe than they were at average breed

weights. But on the present evidence even a very large Blackface ewe at Blythbank would be unlikely to have as high a copper concentration in her blood as a very small Welsh.

Seasonal changes in blood copper levels have been reported by, for example, Butler & Barlow (1963) for flocks in the south-east of Scotland and Allcroft, Clegg & Uvarov (1959) for a flock in Derbyshire. By contrast, Ryley, Harvey, Watson & Levitt (1961) observed no consistent seasonal pattern in the changes in copper concentrations recorded for sheep in the markedly different grazing conditions of Queensland. The seasonal pattern observed by us is confounded by any carry-over effect from copper injection. However, the interesting aspect here is that average changes were shown to be accompanied by changes in variation. Differences showed up more markedly when average levels were low. Among breeds, Blackfaces, for example, changed relatively more in blood copper concentration between summer and winter than did the Welsh (Fig. 1). The class of sheep distinguished by having produced swayback lambs in 1964 differed not only in having, on average, lower levels of copper in their blood, but in having a much more marked seasonal cycle (Fig. 2).

Age effects were significant only in January 1966 when the average copper levels were at their lowest. This is supported by evidence from the same flock in the previous year (Wiener & Field, 1966) when females pregnant for the first time also had significantly lower copper levels than older ewes. Butler & Barlow (1963) observed that the copper levels of young females pregnant for the first time fell more rapidly during pregnancy than those of older ewes—in their case, however, the young females started with a higher initial level. In 1964 the females lambing for the first time had a higher incidence (19 %) of lambs with swayback than older ewes (average 14 %) although the difference was not statistically significant (Wiener, 1966).

The practical importance of copper levels lies in any relationship they may have to performance of the sheep and to risks of disorders associated with deficiency or excess. Indications for deficiency or excess are commonly related to absolute levels in the blood. McCosker (1968), for instance, has shown significant variations from normal (nine Clun Forest or half-bred Suffolk) adult plasma copper levels of forty-eight sheep affected by various disease conditions (sheep from centres in Wales and Cambridge). No account, however, was taken of the possibility that, for example, breed or seasonal factors may have affected the expectation of normality. Far greater differences have been observed in the present study among apparently healthy sheep than those attributed to disease conditions by McCosker. For example, it may be deduced from the results that at Blythbank a 21-month-old Blackface female pregnant for the first time, and of average weight, would be expected on average to have a copper level of 17 μg/100 ml. whole blood in January 1966 compared with 73 μg/100 ml. for an old Welsh ewe also of average weight and also with no previous history of swayback if bled at the same time, or 113 μg/100 ml. if bled on 7 June and barren at that spring's lambing.

Whether the risks of producing swayback lambs are commensurate with the breed differences in copper levels is a question requiring an answer. Among the three pure breeds, and separately among the three cross-bred classes, the previous incidence of swayback ranked inversely to the blood copper levels (Wiener, 1966). The picture is complicated because the heterosis in blood copper levels of the cross-breds is not matched by a correspondingly large advantage in their previous incidence of swayback (the pure breds had 16·1 % of lambs affected, the cross-breds 15·0 %). More specifically, Blackface × Cheviot sheep had a higher incidence of swayback lambs in 1964 (20·6 %) than pure Cheviot (11·4 %) in spite of the higher blood copper concentrations of the former. It seems possible, therefore, that the critical level of maternal blood copper below which swayback lambs would be produced may differ among breeds. This is further supported by our limited evidence that breed differences in blood copper levels also exist among the ewes which themselves produced swayback lambs. Susceptibility of lambs to swayback may therefore be partly independent of the maternal blood copper level.

Arising out of the present study, further communications will deal in greater detail with the variation in seasonal changes and with the separate effects of stage of lactation and week of bleeding in the summer of 1966.

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The incidence of swayback among lambs with particular reference to genetic factors

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SUMMARY

The incidence of swayback among lambs in two flocks, previously reported, was reanalysed by a specially developed modification of the probit analysis technique in order to allow for the joint complications of an all-or-none trait and a large number of possible classifications for the animals in each flock. The form of analysis described yields predictions of the probability of swayback among lambs for the given circumstances.

Breed and sire within breed each affected the probability appreciably even when allowance for live weight of ewe and lamb was made. The effects of live weight, though significant in each flock, were not consistent in direction between the flocks. Other significant factors affecting swayback incidence were the manner of rearing the lambs, week of birth, and, in one flock, the sex of the lamb.

INTRODUCTION

The incidence of swayback among lambs in three genetically diversified flocks was shown to be strongly associated with the breed of sheep and with the sire within breed (Wiener, 1966). A number of other factors were also found to have affected the incidence, notably the week in which the lambs were born, the birth weight of lambs, and under particular circumstances the number of lambs born and reared per ewe. A strong association was also found in the fates of co-twins.

Many of the factors previously studied in relation to the incidence of swayback, however, were inter-related, e.g. breed, live weight and twinning rate. Particularly the effect of mother's weight seemed to deserve further study as a factor influencing the occurrence of swayback lambs. Judged on breed differences, light breeds (e.g. Welsh and Welsh cross) were associated with low swayback incidence and heavier breeds (e.g. Blackface and Blackface cross) with a high incidence. Did breed differences in the incidence of swayback therefore merely reflect weight differences? Within breeds, however, where maternal weight at mating time is often regarded as a guide to the ewe's general condition, the effect of weight was not apparent.

A more detailed statistical analysis of the data is now presented in order to lead to a clearer understanding of the separate significance of different factors associated with the previously reported occurrences of swayback.

MATERIALS AND METHODS

The definition of swayback used and details of the breeding, farm environment and management of the flocks involved have been given previously (Wiener, 1966). The present study is confined to the two flocks contributing most of the data. In both flocks the incidence of swayback being studied occurred in 1964. Essential points are as follows.

Animals

Flock 1. Lambs belonged to three breeds of sheep—Scottish Blackface, Cheviot and Welsh Mountain, and the crosses between them. Crossbred lambs were themselves the offspring of crossbred parents. Both the purebred and the crossbred sheep are represented at different levels of inbreeding (0, 25, 37·5 and 50 %). The ewes were in regular ages from 2 to 5 years old at lambing. The

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flock has been closed to females since 1955 and to males since 1958.

Flock 2. Lambs were derived from 4-year-old Scottish Blackface and a few Blackface × Swaledale ewes. A sample of ewes from each source was mated to each of two rams from each of five breeds, viz. Border Leicester, Clun Forest, Dorset Horn, Finnish Landrace and Merino.

Management

The salient feature is that the different genetic classes in each flock were treated alike. Each flock was run as a single unit without sub-division except as follows:

In flock 1 (at Blythbank, Peeblesshire) ewes were divided from the birth of their lambs to the time of weaning into three sub-groups according to the week of birth of their lambs. These three sub-groups, which were created only for ease of handling, were treated as nearly alike as possible. From weaning to the age of 18 months the young females were kept as a separate group from the ewes but in similar, often adjacent, fields.

In flock 2 (at Broughton Knowe, Peeblesshire) ewes rearing twins were kept until weaning in fields of sown pastures whilst those rearing singles were returned to hill grazing.

Statistical procedure

The (statistically) small sizes of the flocks, coupled with the large number of possible classifications, and the quantal (all-or-nothing) nature of the swayback record, necessitated a rather specialized type of statistical analysis. The way in which the difficulties arise may be illustrated by considering first the analysis appropriate to the results of a simple investigation into the effect of two classification factors (say breed and sex), and one continuous variable x (say birth weight) on a continuous 'dependent variable' y (say mean weekly weight gain to weaning). Such an investigation presents no difficulty. Suppose there are two breeds involved: then lambs are divided into 4 single-sex, single-breed groups, and a linear (or other) regression of y on x calculated initially within each group. Standard statistical procedures are then used to test whether the dependence of y on x within each group is real, whether the slope depends on breed or sex, and, if not, whether the average of y for fixed x depends on either breed or sex. Now consider an experiment involving the same four groups but in which presence or absence of swayback is recorded rather than a continuous y. Within any reasonably large group, lambs can be classified into subgroups, each containing lambs of the same birth-weight (say to the nearest pound), and the percentage of lambs developing swayback can be recorded for each sub-group. The dependence of this percentage on birth-weight can then be explored. This investigation is not a simple regression since percentages must lie between 0 and 100 a simple linear relationship cannot hold, and the correct procedure would be a *probit* (or similar *analysis* (Finney, 1952; Sampford, 1951), leading to a straight-line relationship between the *probit* (a quantity related to the percentage, or probability of swayback, but ranging over all possible negative and positive values as the percentage ranges from 0 up to 100) and the birth-weight (or some function of it). This analysis, though more complex than a simple regression, is also standard. However, now suppose that instead of there being only four possible classifications, there are many—perhaps more, even, than there are lambs: for example, in flock 2 classification by ram's breed, ewe's breed, sex of lamb, type of birth (single or twin), type of rearing and date of birth generates about 1000 possible groups, with fewer than 300 lambs in all. Many of the groups will then have only a few lambs in them, often all with different birth-weights, so that even an orthodox probit analysis is impossible. One must therefore use a modification of the probit analysis method described by Finney (1952; §43). Finney considers only a single group, and a single continuous variable x, so that the model required here is much more complicated than his; nevertheless, the general principle is the same. The model used here is effectively

Probit = (sum of unknown constants representing effects of classification factors)

+ (sum of continuous variables, each multiplied by an unknown constant coefficient).

These constants are literally constant over all lambs, the only difference being in the particular ones that appear in the 'sum of constants' term in the formula. For example, in flock 2 each ram was given a separate constant, as was each sex: then in an analysis taking account of only these two classifications, the 'sum of constants' term for a male lamb sired by ram 3 would be simply

(constant for ram 3) + (constant for males).

The analysis (which is extremely tedious, even on the Elliott 803, the fastest computer conveniently available to the authors when this investigation was undertaken) consists of a maximum likelihood procedure by which all the constants and coefficients are estimated: for a lamb having any particular combination of classification factors the appropriate estimated constants and values of continuous variables can then be substituted into the formula

yielding the probit, and hence (by reference to tables) the probability that such a lamb will develop swayback.

This is, of course, an over-simplified model, but probably not much more so than the usual model used in multivariate linear regression. Goodness of fit can be assessed by a criterion related to χ^2: in the results presented here only those factors are included whose inclusion in the model gave an appreciable improvement in goodness of fit (or, strictly, whose omission made the fit appreciably less good, since the method adopted was to start by including all likely factors, and gradually omit those that were not contributing appreciably to the goodness of fit). The procedure of deciding to include or omit a particular factor can be thought of as a significance test, though it is a rather imprecise one, since the distribution of the quantity on which it is based cannot be exactly determined: for this reason a strict significance level was not adopted, and any factor contributing 'suggestively' to the goodness of fit was given the 'benefit of the doubt', and retained.

The analysis presents another slight, but unavoidable, problem of interpretation. If, for any one classification, none of the lambs in any group develop swayback, the relevant constant is estimated as minus infinity, corresponding to a probability of 0, or virtual impossibility, of developing swayback. Common sense suggests that this conclusion is too sweeping, particularly if the group is small, but it is still the most plausible prediction on the evidence available, and an attempt to replace the value 0 by any other probability can only be arbitrary.

A further, but non-analytic, problem was presented by a number of lambs that died in the first few days of life (still-born lambs were omitted completely). Since swayback can manifest itself at very early ages, there is a case for including all live-born lambs; on the other hand, a lamb that dies at a few days old, from a cause other than swayback, has relatively little chance of developing swayback, so that its inclusion in the analysis will tend to result in underestimates of probabilities of developing swayback. This problem was solved by making all analyses twice, once including and once omitting the lambs dying from non-swayback causes. For many of these lambs no method of rearing was recorded: in the analysis including them, therefore, a further category, 'not known', was added to this classification.

Characters initially considered for both flocks were sex, birth type (single or multiple), rearing (single suckled, twin suckled, hand reared, unknown—see previous sentence), week of birth, birth-weight of lamb, and ewe's tupping weight: the last two were treated as continuous variables. In flock 1 breed of lamb (see Table 1 for classifications), and in flock 2 sire, and breed of dam, were also considered. In exploratory analyses for flock 1, parity of ewe and degree of inbreeding were also considered, but did not appear likely, on the evidence of these analyses, to contribute appreciably to successful prediction of swayback, and so were not included in the main analyses.

Table 1. *Probit lines yielding the probability of the occurrence of swayback among lambs in flock* 1. *Basic line* (y = *probit* − 5) *for single-born, single-reared Blackface lambs born in the first week of lambing*

	All lambs	Live-born lambs excluding recorded non-swayback deaths
Basic line*	$y = 1{\cdot}72 - (0{\cdot}0084 \times$ ewe's wt (lb) at mating)	$y = 2{\cdot}39 - (0{\cdot}0118 \times$ ewe's wt (lb) at mating)
Adjustment constants (to be added to constant term in basic line)		
Breed: Cheviot	−1·32	−1·55
Welsh	(−infinity)†	(−infinity)†
Cheviot × Welsh	−2·05	−2·41
Blackface × Welsh	−1·48	−1·85
Blackface × Cheviot	−0·97	−1·26
Reared as twin	−0·12	—
Hand-reared	(−infinity)†	—
Rearing unrecorded‡	−1·41	—
Week of birth 2	−0·42	−0·37
3	−0·51	−0·52
4	+0·02	+0·02
Later	(−infinity)†	None

* Basic line described in title.

† An estimate of (−infinity) arises from the absence of any swayback lambs in the appropriate class and corresponds to a zero probability of getting swayback.

‡ Mostly lambs dying in first few days after birth.

RESULTS

Flock 1

The factors found to have contributed appreciably to variation in the incidence of swayback, and so retained in the final model, were breed, ewe's weight at mating, the type of rearing of the lambs and their week of birth.

The basic probit line for flock 1 is given in Table 1, and relates to single Blackface lambs born in the first week of lambing, and reared as singles. The formula enables the probability of swayback among lambs having these properties, and born to ewes of particular weights, to be estimated. For example, with a ewe of weight 120 lb the formula in the left-hand column leads to a value of

$$1{\cdot}72-(0{\cdot}0084\times 120)\ =\ 0{\cdot}71$$

for y, corresponding to a probit of 5·71: reference to a table of probits against percentages (e.g. Finney,

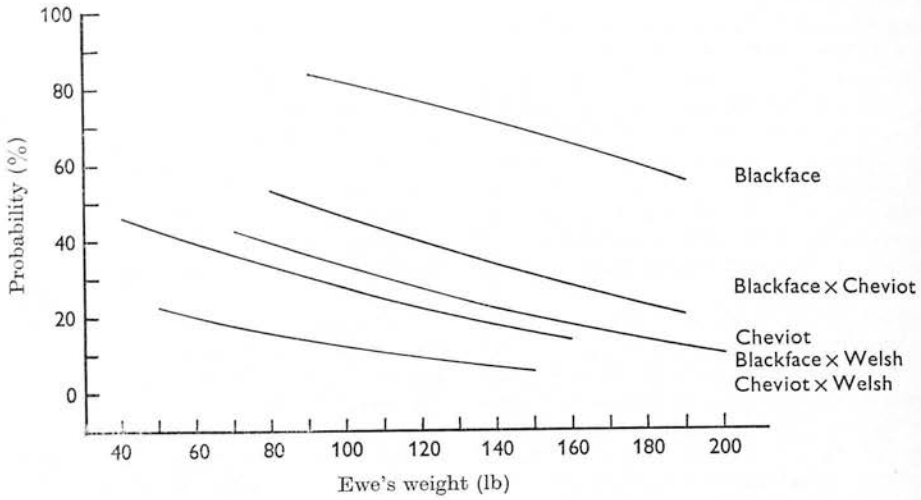

Fig. 1. The estimated probability of swayback among all lambs of five breeds in flock 1, according to weight of dam at time of mating. (A sixth breed, the Welsh Mountain, produced no swayback lambs, giving an estimated probability of zero for that breed regardless of weight of dam).

Table 2. *Probit lines yielding the probability of the occurrence of swayback among lambs in flock* 2. *Basic line* (y = *probit* -5) *for single-reared female offspring of Ram* 1

		All lambs	Live-born lambs excluding recorded non-swayback deaths
Basic line*		$y=-1{\cdot}43-(0{\cdot}206\times$ lamb's birth wt (lb)$)$ $+(0{\cdot}0216\times$ ewe's wt (lb) at mating	$y=-1{\cdot}47-(0{\cdot}285\times$ lamb's birth wt (lb)$)$ $+(0{\cdot}0310\times$ ewe's wt (lb) at mating
Adjustment constants (to be added to constant term in basic line)			
Ram no.	Sire's breed		
2	Border Leicester	(−infinity)† (−)	(−infinity)† (−)
3	Clun Forest	0·12, 0·62 0·37	0·02, 0·20 0·11
4			
5	Dorset Horn	−0·46, −0·02 −0·24	−0·80, −0·49 −0·64
6			
7	Finnish Landrace	−0·55, 0·33 −0·11	−0·97, −0·02 −0·50
8			
9	Merino	−0·53, −0·61 −0·57	−0·69, (−infinity)† (−)
10			
Male lambs		0·36	0·52
Reared as twin		−1·56	−1·87
Rearing unrecorded‡		−0·23	—

* Basic line described in title.
† ‡ See footnotes of Table 1.

1952; Table 1) shows that this corresponds to a probability of 76 % of developing swayback under the conditions of flock 1 in 1964. Adjustments are given for factors producing deviations from the basic line: these are to be added to the constant term in the basic formula. The negative sign attached to the constants indicates that all classes (with the minor exception of the late-born lambs) had a lower probability of producing swayback symptoms than the Blackface singles in the basic class. For example, a Cheviot lamb whose dam weighed 120 lb, and born in the second week, and reared as a single, would have a y-value of

$$1{\cdot}72 - 1{\cdot}32\ [\text{'Cheviot' adjustment}] - 0{\cdot}42\ [\text{'week 2' adjustment}] - (0{\cdot}0084 \times 120) = -0{\cdot}02 - 1{\cdot}01 = -1{\cdot}03,$$

or a probit of 3·97, corresponding to a probability of only 15% of developing swayback. Within breeds, the probability of a lamb showing swayback symptoms declined with increasing ewe's weight. This is in the opposite direction to the 'weight effect' suggested by average breed differences.

One set of figures in Table 1 refers to all lambs born in flock 1, the other set to live-born lambs which did not die for reasons other than swayback. Inevitably the over-all probability of a lamb showing swayback symptoms is higher in the latter case, but the contribution of the separate breeds and other factors are similar in both sets of data. Thus, for example, the relative effects of breed on susceptibility to swayback have not been falsified by deaths from other causes, as might have been expected to happen if 'other' deaths were high in some, but not other, breeds.

Probit values calculated from the formulae in Table 1 have been converted, by way of example, into percentages of lambs likely to be affected by swayback for different breed classes and live weights of ewe. In the example illustrated in Fig. 1, the lines refer to single-born, single-reared lambs born in the first week of lambing. The results for each breed have been extrapolated to include the actual weight range of each breed of ewe in the flock.

Flock 2

The significant factors in this flock were sire, ewe's weight, lamb's birth weight, sex of lamb and type of rearing. There were substantial differences on average between sires of different breeds, but no greater than those between sires of same breed (there were two sires from each of the five breeds). In other words, the apparent differences due to breed of sire could well have arisen purely by chance, as a consequence of the particular selection of sires made for this experiment: a different set of sires could have produced quite different apparent breed effects. Table 2 shows results in terms of probits. The basic probit line yields the probability of swayback for female offspring of ram No. 1 (a Border Leicester) reared as singles. Birth weight and ewe's weight are included in the basic line. Adjustment

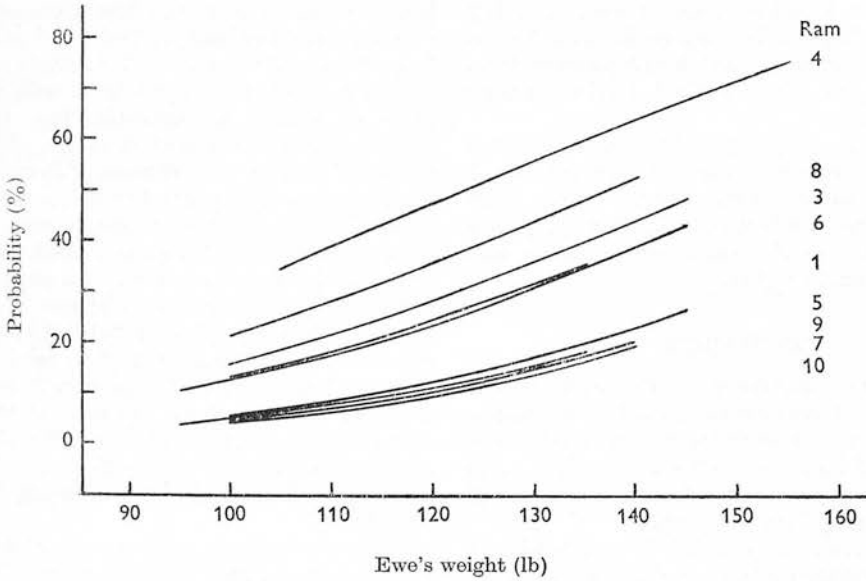

Fig. 2. The estimated probability of swayback among all the offspring of nine rams (a tenth ram had no swayback offspring) from five breeds in flock 2, according to weight of dam at time of mating. Birth-weight of lamb standardized to 9 lb.

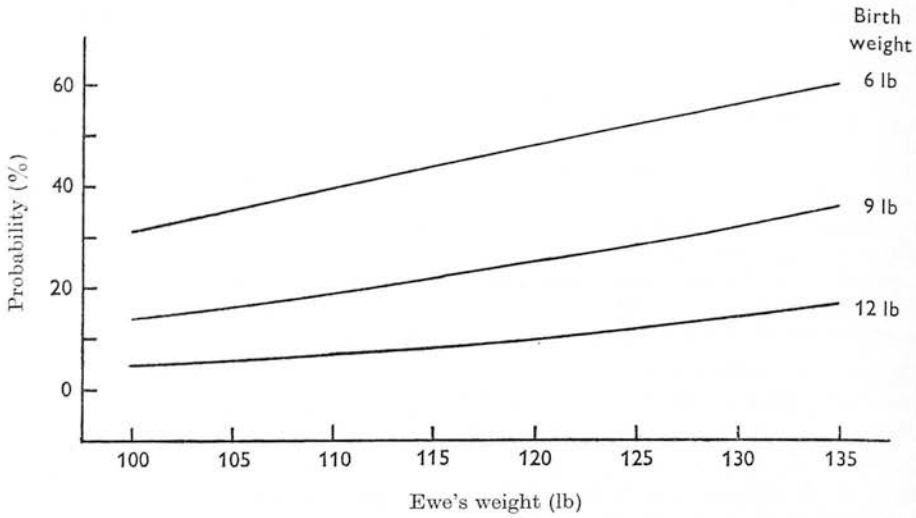

Fig. 3. The estimated probability of swayback among all the offspring of Ram 1 in flock 2, according to weight of dam at time of mating and birth weight of lamb.

constants are given for the other sires, for sex of lamb and type of rearing. Heavier ewes in this flock had a greater probability of producing swayback lambs. This is the opposite of the weight effect in flock 1. Possible reasons for the difference will be discussed later. Heavier lambs, however, had a lower probability of swayback symptoms than lighter ones. In other respects the results for all lambs and for lambs excluding non-swayback deaths parallel those from flock 1. The 'rearing' effect is seen to have been much greater in flock 2 than in flock 1, possibly because in flock 2 ewes rearing twins were kept on different pastures from ewes with singles, whilst in flock 1 all ewes were kept together.

Figure 2 gives an example of the results related to single-reared female lambs of 9 lb weight; Fig. 3 shows the probability that a single female lamb sired by ram no. 1 will show swayback symptoms for three birth weight categories of lamb and different maternal weights.

DISCUSSION

The most important feature of the results is that breed and sire effects were shown to be statistically significant even after adjusting for effects of weight of ewe and of lamb. The effects were large and yielded probability estimates for the occurrence of swayback varying from 0 to 80 %.

The breeds involved in flock 1 differed markedly in body size; for example, ewes of the Welsh breed weighed only about two-thirds as much as those of the Blackface breed (Wiener, 1967). The general effect of body weight as deduced from breed would be for the probability of swayback to increase wi the live weight of the maternal breed. Within bree however, the effect of weight of ewe in flock 1 w seen to be in the opposite direction—namely for t lighter ewes to have had the higher probability producing swayback lambs.

This effect of mother's weight is not apparen valid as a generalization since it goes in the opp site direction in flock 2, where, however, the ligh lambs were shown to run a greater risk from swa back than the heavier ones. The effects of weight ewe and weight of lamb in flock 2 will go some w toward cancelling each other, and within t observed range of ewe and lamb weights the t effect of weight is uncertain. The discrepan between flock 1 and flock 2 in the effect of l weight of ewe on the incidence of swayback nee consideration. The possibility exists that the di ferent farm environments may be responsible f different responses of the sheep. Differences cou also arise because flock 1 with its several breed ages, and inbreeding classes of ewe covers a l wider weight range of ewe (46–196 lb) than flock (95–155 lb), which consisted of predominantly o breed of dam and a single age class. There is, ho ever, no evidence from the original unadjus data that the within-breed association of weight ewe and incidence of swayback among the lam differs significantly for the different breeds flock 1.

Studies in flock 1 on the concentration of copp in the blood, a factor known to be associated w the occurrence of swayback (e.g. Barlow *et al.* 19 showed that ewe's weight, within breeds, w positively related to copper concentration in t

blood, i.e. the heavier the ewe the higher the copper concentration (Wiener, Field & Wood, 1969). This at any rate agrees with the weight–swayback relationship reported for the same flock in this paper. At the breed level the relationship is also consistent with the finding that the lightest breed, the Welsh, had amongst the highest average blood and liver copper level (Wiener & Field, 1966, 1969) and the much heavier Blackface the lowest copper levels.

We are indebted to Dr J. A. Watt, Edinburgh School of Agriculture, and Dr R. M. Barlow, Moredun Research Institute, for the diagnosis of swayback cases and to Mr J. C. Harris and Mr E. Hughes, who supervised the sheep and made observations.

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The concentration of minerals in the blood of genetically diverse groups of sheep

II. Calcium, phosphorus, magnesium, potassium, sodium and chlorine concentrations for three hill-breeds and their crosses at pasture

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SUMMARY

Three-hundred and thirty-four female sheep of the Blackface, Cheviot and Welsh Mountain breeds and the crosses among these breeds kept as one flock at pasture were bled in September 1966. Concentrations of Ca, Mg, K, Na and Cl were determined on plasma and P on whole blood. Mean concentrations (mg/100 ml) were: Ca 9·65; P 5·54; Mg 2·02; K 23·2; Na 345; Cl 365; and coefficients of variation (%) 11·1, 18·1, 29·0, 10·5 6·7 and 2·3 respectively.

Breed was a highly significant ($P < 0·01$) source of variation for Ca, P, Mg and Cl, but except for Mg, the contribution to the total variance was small (< 10 %). Average values for cross-bred ewes deviated significantly ($P < 0·05$) from those of pure-bred for Ca and P concentration. Live-weight, within class, had a small but significant effect on Ca and Mg concentration.

The concentration of Ca and Mg declined very significantly with age of ewe, there was a similar trend for K, while P showed a slight but steady tendency to increase with age, and Cl showed a more erratic increase.

For Ca, barren ewes had a lower concentration (−0·44 mg/100 ml) than ewes with lambs whilst ewes with single lambs at birth had lower concentrations (−0·35) than ewes with twins. Other factors with effects too large to be ignored ($P < 0·1$) were the interaction of breed × no. of lambs (K and Cl) and swayback history (Cl).

INTRODUCTION

The present paper deals with the concentrations of a number of minerals in the blood plasma (whole blood for phosphorus) of sheep in a grassland flock comprising the Scottish Blackface, Cheviot and Welsh Mountain breeds and their crosses. The background to this work was described in an earlier paper dealing with blood copper concentrations W iener, Field & Wood, 1969).

MATERIALS AND METHODS

The flock comprised the three pure-breeds and their crosses (see above) each at various levels of inbreeding from 0 to 50 %. The animals were born and bred on the farm and managed as one flock since 1955. Five age classes were represented among the ewes. Twenty ewes remained in the flock from among those which had produced swayback lambs in 1964. Each January since 1965 ewes have been injected with copper to reduce risks of further swayback. Further details were given by Wiener (1967) and Wiener, Field & Wood (1969).

The sheep were bled for the present experiment in September 1966. The numbers were: Blackface 32; Cheviot 33; Welsh Mountain 48; Blackface × Cheviot 65; Blackface × Welsh 86; Cheviot × Welsh 70.

Estimation of mineral concentrations

Blood samples were obtained from the jugular vein using an evacuated heparinized tube (Becton, Dickinson Ltd., Drogheda, Eire) and a protein-free filtrate of whole blood was obtained immediately using trichloro-acetic acid (10% w/v) as the protein precipitant. P was determined in the filtrate by the method of Fiske & Subbarow (1925). Plasma was obtained by centrifugation and the cations determined by the following methods: Ca and Mg (Suttle & Field, 1969), Cl (Technicon Auto-Analyser method N-5b) and Na and K by atomic absorption and flame photometry respectively after suitable dilution.

Statistical analysis

This consisted of fitting a linear model with parameters representing the effects of breed, inbreeding, live weight of ewe (in January 1966), swayback history, aspects of lambing performance, date of lambing and age of ewe, as well as a number of interactions.

The final model includes the parameters with effects significant at the 10% level of probability except in the case of the effects of age of ewe. Age was analysed in two parts (i) as the difference between the youngest age group (2-year-old) and the average of the older ones and (ii) as variation among the four older age classes (3–6-year-old). If one or other of these analyses showed statistically significant effects both were included in the final analyses. Further details on the form of the analysis and the criteria for eliminating factors not retained in the final model were given by Wiener, Field & Wood (1969).

The final statistical model differed for each mineral. The appropriate factors for each mineral are represented by entries in Table 1. The term 'factor' is used to represent the joint contribution of number of parameters e.g. the factor 'breed' is represented by the parameters for the three separate breeds and the three cross-bred types.

When live weight of ewe was found to have had a significant effect, with other factors constant, the analysis was repeated with weight excluded from

Table 1. *Factors included (with the exception of live weight)* in the final model of the statistical analysis of each mineral, and for each factor the proportion of the total variation* (% SS) *for which it accounted and the level of significance of its effect.*

Absence of an entry indicates that the factor was not included in the final model—other factors than those listed also had no significant effects, see text.

		Mineral					
		Calcium	Phos-phorus	Magne-sium	Potas-sium	Sodium	Chlorine
Breed	SS (%)	4·4	9·3	20·2	—	—	4·3
	$P <$	0·01	0·001	0·001	—	—	0·01
Inbreeding	SS (%)	—	2·7	—	—	—	—
	$P <$	—	0·05	—	—	—	—
2-yr-old *v.* older	SS (%)	3·3	1·1	10·8	0·6	—	0·1
	$P <$	0·001	0·1	0·001	0·2	—	($P > 0·5$)
Age (within older)	SS (%)	1·1	0·5	5·1	2·1	—	3·2
	$P <$	0·3	($P > 0·5$)	0·001	0·1	—	0·01
Barren	SS (%)	1·5	—	—	—	—	—
	$P <$	0·05	—	—	—	—	—
No. of lambs at birth	SS (%)	2·3	—	—	—	—	—
	$P <$	0·01	—	—	—	—	—
Interaction (Breed × no. lambs)	SS (%)	—	—	—	3·5	—	2·8
	$P <$	—	—	—	0·05	—	0·1
Swayback history	SS (%)	—	—	—	—	—	1·0
	$P <$	—	—	—	—	—	0·1
Live weight when other factors constant	—	†	—	†	—	—	—

* The effect of live weight was not removed as a source of variation in the partitioning of variation attri table to the other factors.

† Regression of mineral concentration on live weight found to be a significant source of variation ($P < 0·$ when included along with the other factors shown.

the final model. This enabled estimates to be presented for each class (e.g. Blackface) at its own average weight, but the residual regression of mineral concentration on weight, where appropriate, to be given in addition.

RESULTS

Table 1 shows the contribution of various factors to the variation in mineral concentration and the significance of the effects of these factors. Factors without significant effect on any of the minerals are not shown.

Among the factors considered, breed and age were the most significant sources of variation. The proportion of the total variation accounted for by the various factors is affected by the number of variables included in the statistical model, but the results suggest appreciable differences between minerals. For example, breed accounted for approximately 4 % of the variation in Ca concentration but 22 % of that in Mg.

The mean values for concentration of each mineral are shown in Table 2 and appear to be normal. Variability was not, however, proportional to the mean. Expressed as the coefficient of variation, Mg concentration was more than twice as variable as the concentration of Ca and more than eleven times as great as that of Cl. Two coefficients of variation are shown in Table 2, one relative to the overall variation (and overall mean) observed in this genetically diverse flock, the other relative to the residual variation and the adjusted mean remaining when the variation attributable to the factors shown in Table 1 had been removed.

Further results are presented separately for each mineral in relation to the factors shown for each in Table 1. The effects of parameters are presented as deviations from particular averages. These deviations can be related to the overall average values for each mineral shown in Table 2.

Table 2. *Mineral concentrations (mg/100 ml) and variability in the plasma of sheep's blood (whole blood for phosphorus)*

	Overall		Coefficient of variation (%)	
	Mean	S.E.	Overall	Residual†
Calcium	9·65	0·06	11·1	10·8
Phosphorus*	5·54	0·05	18·1	16·7
Magnesium	2·02	0·03	29·0	26·1
Potassium	23·16	0·13	10·5	10·4
Sodium	345·4	1·3	6·7	(6·7)
Chlorine	364·9	0·5	2·3	2·2

* In whole blood.

† Residual S.D. in relation to adjusted flock mean.

Calcium

The effects of breed, age of ewe and number of lambs born, and the effect of live weight are shown in Table 3. Welsh Mountain sheep had more Ca in their blood than the Cheviot or Blackface females, and crosses with the Welsh had a significantly higher concentration ($P < 0{\cdot}05$) than crosses of Blackface with Cheviot. The lower values for the Blackface and its crosses did not differ significantly from the values of the Cheviot. The results suggest that the cross-breds had the concentration of the parent breed with the higher value. Thus on average, cross-breds had slightly (0·28 mg ± 0·12) more Ca per 100 ml blood plasma than pure-breds.

Table 3. *Calcium concentration in blood plasma (mg/100 ml)*

The effects of breed, age, and lambing performance, and the effect of live weight when other factors were held constant.

	Mean	S.E.*
Deviations from the average of the breeds of		
Blackface	−0·37	0·19
Cheviot	−0·17	0·17
Welsh	0·12	0·15
Blackface × Cheviot	−0·13	0·13
Blackface × Welsh	0·29	0·12
Cheviot × Welsh	0·26	0·12
Average difference of cross-bred *minus* pure-bred†	0·28	0·12
Deviations from the average of 3–6-year-old ewes of age (years)		
2	0·47	0·13
3	0·17	0·12
4	0·13	0·13
5	−0·00	0·12
6	−0·30	0·20
Barren ewes as deviation from ewes with lambs at birth	−0·44	0·19
Ewes with lambs at birth		
1 lamb	−0·18	0·09
2 lambs	0·18	0·09
Residual regression on live-weight of ewe (lb)‡	0·009	0·003

* Standard errors have been adjusted to allow for covariance, and can be used to obtain approximate S.E.'s of differences within any classification. For example, S.E. of difference between Blackface and Cheviot Ca values is estimated by

$$\pm\sqrt{(0{\cdot}19^2+0{\cdot}17^2)}$$

† Difference between adjusted means of breed groups (not for use as an adjustment constant).

‡ The residual effect of live weight was computed separately from the rest of the model. The estimates of the effects for each other class are those applicable to animals of the average weight for that class.

Young ewes (2-year-olds) had a higher Ca concentration in their blood than older ones; a steady age trend is also seen among the age classes of the older sheep.

Ewes giving birth to twins 5 months previously had $0{\cdot}35 \pm 0{\cdot}12$ mg/100 ml more Ca in their blood than ewes with single lambs at birth and ewes with lambs, in turn, had higher concentrations ($0{\cdot}44 \pm 0{\cdot}19$) than barren ewes.

Live weight, when other factors were constant, had a small but significant effect on Ca concentration. The heavier the sheep within its class the higher the Ca concentration (0·009 unit of Ca/1 lb increase in body weight). At equal weights of ewe, breed variation in Ca concentration was greater than at average weights for each breed and specific differences were more marked. For example the differences in Ca concentration between a heavy Welsh and a light Blackface ewe would be expected to be appreciably larger than that deduced from the corresponding breed difference in Table 3.

Inbreeding was not a significant source of variation when judged by variation among the inbreeding classes. The estimates of the inbreeding effects (0·22, −0·05, 0·08, −0·25 mg Ca/ml for 0, 25, 37½ and 50 % inbreeding respectively) showed a decline in concentration with inbreeding suggestive of a genetic trend. This change in Ca concentration may, however, be a consequence of an associated change in live weight since no change with inbreeding could be observed when live weight was held constant.

Phosphorus

The ranking of breeds for P (Table 4) tended to be the reverse of that for Ca. The Blackface and its crosses had the highest values, the Welsh and its associates the lowest; Cheviots were intermediate. Cross-bred sheep on average, had lower concentrations than the pure-bred.

The breeding system used in the flock affected P variation but showed no systematic trend in the scale from non-inbred to 50 % inbred sheep.

Young ewes, on average, had somewhat lower concentrations ($P < 0{\cdot}1$) than older ones, and up to 5 years of age, there was a regular, though small, increase in concentration. The differences among the four oldest age classes did not, however, contribute significantly to variation.

Magnesium

The analysis showed far greater variation for this mineral than for the others (see Table 2); in consequence, some differences which appeared large were not necessarily highly significant.

Breed variation shown in Table 5, was highly significant ($P < 0{\cdot}001$) the most marked aspect being the low values of the pure Cheviot and the

Table 4. *Phosphorus concentration in whole blood (mg/100 ml)*

The effects of breed, inbreeding, and age.

	Mean	S.E.*
Deviations from the average of the breeds of		
Blackface	0·71	0·17
Cheviot	−0·06	0·16
Welsh	−0·28	0·13
Blackface × Cheviot	0·16	0·12
Blackface × Welsh	−0·15	0·11
Cheviot × Welsh	−0·38	0·12
Average difference of cross-bred *minus* pure-bred†	−0·25	0·11
Deviations from the average of inbreeding (%)		
0	−0·30	0·11
25	0·02	0·10
37½	−0·12	0·15
50	0·40	0·26
Deviations from the average of 3–6-year-old ewes of age (years)		
2	−0·25	0·13
3	−0·10	0·12
4	−0·03	0·12
5	0·11	0·11
6	0·02	0·18

* † See Table 3 for explanation.

Table 5. *Magnesium concentration in blood plasma (mg/100 ml)*

The effects of breed and age and the effect of live weight when other factors were held constant.

	Mean	S.E.*
Deviations from the average of the breeds of		
Blackface	0·24	0·09
Cheviot	−0·35	0·08
Welsh	0·23	0·07
Blackface × Cheviot	0·08	0·06
Blackface × Welsh	0·19	0·06
Cheviot × Welsh	−0·40	0·06
Average of difference of cross-bred *minus* pure-bred†	−0·08	0·06
Deviation from the average of 3–6-year-old ewes of age (years)		
2	0·45	0·06
3	0·25	0·06
4	0·04	0·06
5	−0·01	0·05
6	−0·28	0·09
Residual regression on live-weight of ewe (lb)‡	0·0032	0·001

* † ‡ See Table 3 for explanation.

Cheviot × Welsh crosses. Blackface values were almost the same as those of the Welsh. No obvious generalization arises from the results of cross-breeding. Values for the Cheviot × Welsh cross were at the low level of the Welsh but the Cheviot cross with the Blackface gave a value intermediate between the pure breeds and the Blackface × Welsh value also did not deviate significantly from the mid-parent value.

Inbreeding was not a significant source of variation although the 50 % inbred sheep had a higher concentration ($0{\cdot}30 \pm 0{\cdot}15$ mg/100 ml) than non-inbred or the other two classes of inbreds (which in turn did not differ from the non-inbred or from each other). However, when weight was held constant there was a steady, though not linear, increase in Mg concentration with increasing inbreeding (the effects being $-0{\cdot}14$; $-0{\cdot}10$; $-0{\cdot}05$; $0{\cdot}29$ for 0, 25, $37\frac{1}{2}$ and 50 % inbreeding respectively). When weight was held constant variation attributable to inbreeding approached significance ($P < 0{\cdot}1$).

Age had a marked effect on Mg concentration, the youngest sheep having about 40 % more per unit volume of blood than the oldest ones.

There was a small but significant ($P < 0{\cdot}01$) regression of Mg concentration on live weight ($0{\cdot}003 \pm 0{\cdot}0015$ units Mg/1 lb increase in live weight) when breed and age effects were constant. Breed variation was not much affected by holding live weight constant.

Table 6. *Potassium concentration in blood plasma (mg/100 ml)*

The effect of an interaction of breed × no. of lambs born and the effect of age.

	Mean	S.E.*
Ewes with single lambs as a deviation from flock average§ for		
Blackface	−0·30	0·49
Cheviot	−0·04	0·50
Welsh	−0·84	0·43
Blackface × Cheviot	0·38	0·39
Blackface × Welsh	−0·13	0·32
Cheviot × Welsh	0·93	0·36
Deviations from the average of 3–6-year-old ewes of age (years)		
2	0·43	0·30
3	0·57	0·28
4	0·21	0·30
5	−0·40	0·27
6	−0·38	0·43

* See Table 3 for explanation.

§ Deviations for ewes with twin or triplet lambs at birth take the same values with the *opposite* sign.

Potassium

There was a slight downward trend in concentration with increasing age, the change, however, was small and not in regular steps (Table 6).

The only effect to be statistically significant ($P < 0{\cdot}05$) was the interaction of breed with the number of lambs born (Table 6) although neither of the corresponding main effects showed any significant differences. The interaction arose from the fact that for the Blackface, the Welsh and the Blackface × Welsh breeds, ewes with single lambs at birth had lower concentrations of K (5 months later) than ewes which had borne twins, whilst the opposite was true for Cheviot × Blackface and Cheviot × Welsh ewes. Pure Cheviot females had a very slightly lower concentration when they had had a single lamb. On average the difference between ewes with singles and twins was the opposite for pure-bred and cross-bred (Table 6).

Table 7. *Chlorine concentration in blood plasma (mg/100 ml)*

The effects of breed, breed × no. of lambs interaction, age and swayback history.

	Mean	S.E.*
Deviations from the average of the breeds of		
Blackface	−1·9	1·5
Cheviot	−3·3	1·4
Welsh	3·1	1·2
Blackface × Cheviot	1·5	1·0
Blackface × Welsh	0·2	0·9
Cheviot × Welsh	0·4	1·0
Average difference of cross-bred *minus* pure-bred†	1·4	1·0
Ewes with single lambs§ as a deviation from the average of the breeds of		
Blackface	−3·6	1·5
Cheviot	0·5	1·5
Welsh	−0·0	1·3
Blackface × Cheviot	0·6	1·1
Blackface × Welsh	1·8	0·9
Cheviot × Welsh	0·9	1·1
Deviations from the average of 3–6-year-old ewes of age (years)		
2	−0·4	1·0
3	−1·0	1·0
4	−1·7	1·1
5	2·5	0·9
6	0·2	1·6
Ewes with swayback lambs in 1964 as deviation from ewes with normal lambs	−4·0	2·1

* † See Table 3 for explanation.

§ Deviations for ewes with twin or triplet lambs at birth take the same values with the *opposite* sign.

Sodium

None of the factors considered had any significant effect on the variation of Na concentration in the blood plasma. The effect of age came nearest to showing a trend in as much as the two youngest groups of sheep appeared to have higher concentrations than the older ones. The results are not tabulated.

Chlorine

Results are summarized in Table 7.

Although there was relatively little variability in this blood constituent (cf. Table 2) breed variation was highly significant. Among the pure-bred sheep, Blackfaces and the Cheviots had very similar values but the Welsh had higher concentrations. On average the cross-breds had 1·4 mg more Cl per 100 ml blood plasma than the pure-bred sheep, but this difference was not statistically significant.

Although the number of lambs born had no significant effect on Cl concentration, there was a suggestion ($P < 0{\cdot}1$) of a breed × number of lambs interaction.

Among the ewes three-years-old or older there was significant age variation in Cl concentration and although the 2-year-old females, on their own, did not differ significantly from the average of the older, they contributed to the tendency for young sheep to have lower concentrations of Cl than other sheep.

The twenty ewes which, 2 years previously, had produced lambs affected by swayback had 4 mg less Cl/100 ml blood plasma than normal contemporaries, a difference close to significance at the 5 % level of probability.

DISCUSSION

There are many publications on the mineral requirements of farm animals in relation to growth, production and health (e.g. Agricultural Research Council, 1965; Underwood, 1966) and on the disorders consequential on deficiency or excess (e.g. Blaxter, 1959, 1960, 1961; Allcroft, 1962, 1964; Underwood, 1966). There is, however, very little information to show whether any of the variability in mineral concentration of animal tissue is inherited and whether the requirements for minerals of genetically different animals within a species are the same. Meyer (1966) suggested the likelihood of such genetic differences citing evidence of individual variation for cattle, pigs and hens. Specific instances of metabolic disorders in cattle, associated with breed differences were suggested by the survey data of Leech, Davis, MacRae & Withers (1960) for hypomagnesaemic tetany and acetonaemia. For sheep the incidence of swayback (enzootic ataxia) was found to be associated with genetic factors (Wiener, 1966) and was later also shown to be associated with breed differences in copper concentration in blood (Wiener & Field, 1966; Wiener, Field & Wood, 1969) and in liver (Wiener & Field, 1969).

Genetic effects. The evidence presented in this paper of differences among breeds and crosses of breeds in the concentrations of Ca, P, Mg and Cl says relatively little about the mode of inheritance. For Ca and P concentrations, the values of the cross-bred sheep deviated significantly from mid-parental values and suggest that non-additive genetic variation is involved. There is, however, little evidence for regular change with inbreeding nor reliable evidence for absence of such change. No sound basis thus exists for a further hypothesis about the nature of any non-additive variation. Mg concentration came nearest to showing a steady change with inbreeding (an increase) consistent with a lower average value for cross-breds compared with pure-breds. These effects, however, failed to reach statistical significance except when live weight of ewe was held constant.

For P (and to a lesser extent for Mg) the cross-breds, on average, had lower values than the pure-bred sheep. The biological significance of such negative heterosis is difficult to see unless in the case of P it is the result of a compensatory effect to the correspondingly higher concentration of Ca among cross-breds.

Eighteen of the 20 Mg concentrations recorded with values below 1 mg/100 ml blood plasma were from Cheviot or Cheviot crosses. Breed differences in susceptibility to hypomagnesaemia thus appear possible. These very low values of Mg were not associated with very low values of Ca except in two animals with Ca below 7 mg/100 ml. The breed difference in Mg may not therefore indicate any difference in susceptibility to hypomagnesaemic tetany, since the latter is also largely associated with hypocalcaemia (Hemingway & Ritchie, 1966).

Ritchie & Hemingway (1963) have reported Cheviot sheep to have lower Ca and Mg concentrations than Cheviot × Border Leicester crosses. A breed difference in the concentration of Ca in Southdown and Welsh Mountain female sheep around 9–12-month-old has recently been reported by Sykes, Field & Slee (1969), but the possibility cannot be excluded that this difference arose from the different environments of the sheep up to about 5 months old. In a number of other experiments where different breeds were involved, breed differences were either not observed or not reported, possibly because of factors confounded with breed.

Live weight. The slight but significant positive regressions of Ca and Mg concentrations on live weight raise the possibility that greater growth

within breed and age group was achieved as a consequence of higher concentrations of these minerals. To test this hypothesis is, however, outside the scope of this paper.

Lambing performance. The higher concentrations of Ca in the blood plasma of ewes which had given birth to twin lambs 5 months earlier compared with ewes having singles or no lambs are clearly negatively related to the stresses of pregnancy and lactation. During lactation, Hemingway, Ritchie, Rutherford & Jolly (1963) found ewes with single lambs to have had higher Ca concentrations than ewes with twins.

Age effects. Among the effects reported here, age effects are the best documented in the literature, but not always with consistent results. For Ca, Hemingway *et al.* (1963) in agreement with our findings, reported higher concentrations for young than for older sheep, as did Long, Ullrey, Miller, Vincent & Zutaut (1965) for the age range from birth to 2 years. Age was found to have no effect on Ca by Vrzgula & Gdovin (1966), Becker & Smith (1950) and Hackett, Gaylor & Bustad (1957).

Becker & Smith (1950), Beeson, Terrill & Bolin (1944) and Vrzgula & Gdovin (1966) all found a decline in plasma inorganic P concentration with age, in contrast to our observation of a slight but steady increase in total P in whole blood. Long *et al.* (1965) observed an increase from birth to 5 days of age followed by a decline to about 2 years.

The decline in Mg concentration with age observed here is supported by evidence of Vrzgula & Gdovin (1966) and Hemingway, Inglis & Ritchie (1960), but is contrary to some later observations of Hemingway *et al.* (1963). Long *et al.* (1965) claimed an increase in Mg concentration during growth and with gestation.

Variability. Average levels of mineral concentration were consistent with published normal values, Long (1961). The lowest variability was found for the elements, Na and Cl (in plasma) with a major role in maintaining osmotic pressure, whilst the highest variability and also the most obvious genetic differences were observed for the three minerals, Ca, P, and Mg, most often associated with deviations from normal growth, health and performance.

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The concentration of minerals in the blood of genetically diverse groups of sheep

III. Correlations among calcium, phosphorus, magnesium, potassium, sodium, chlorine, and copper concentration

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SUMMARY

Two sets of correlations among blood mineral concentrations were calculated (1) those attributable to the effects of various factors (breed, age, lambing performance, etc.) and (2) those remaining (residual) when the effects of such factors had been removed as sources of variation in mineral concentration (the equivalent of correlations within subclasses).

Correlations arising from breed differences in mineral concentrations were highest for Ca.P (−0·81), Ca.Cu (0·83) and P.Cu (−0·95). Correlations consequent on changes with the age of the sheep were most marked for Ca.Mg (0·97, $P < 0·01$) and Cu.K (−0·92, $P < 0·05$) and approximately 0·8 ($P < 0·1$) for Ca.K, P.Mg, P.K and K.Cl.

Residual correlations were all below 0·2 (although seven of the twenty-one were statistically significant, $P < 0·05$) suggesting that within subclasses most of the variation in the concentration of any one mineral was independent of that in the other minerals. Simple and partial correlations were very similar in magnitude suggesting that the associations found between pairs of minerals were not attributable to joint co-variance with any of the other five minerals.

As the sheep grew older, changes in the concentrations of Ca, P and Mg were significantly correlated with the increases in live weight. Within subclasses, differences among the sheep in live weight were significantly ($P < 0·05$) and positively correlated with differences in the concentrations of Ca (r, 0·11), Mg (0·13) and Cu (0·11).

INTRODUCTION

Reports of correlations among mineral concentrations in the blood of apparently normal ruminants are rare in the literature. A study of blood minerals in Guernsey cows by Lane, Campbell & Krause (1968) produced a number of small (< 0·18) but statistically significant correlations.

Evidence on the inter-relations of seven minerals (Cu, Ca, P, Mg, K, Na and Cl) with each other and with live weight in a genetically diverse flock of sheep, are examined in this paper.

MATERIALS AND METHODS

The flock comprised the Scottish Blackface, Cheviot and Welsh Mountain breeds and the crosses among them. Three-hundred and twenty-four female sheep had data on the concentrations of all seven minerals.

Correlations were calculated using the Cu values of 7 June 1966 (Wiener, Field & Wood, 1969) and the values of other minerals from blood samples obtained in September 1966 (Field, Wiener & Wood, 1969). Cu and P were determined for whole blood, the other minerals for blood plasma.

The calculation of correlations required a common linear model to be applied to the concentration of each mineral and to live weight. Accordingly, the effects of breed, inbreeding, age, number of lambs born per ewe in 1966, week of lambing and swayback history, were estimated for each mineral although not each of these factors had

had statistically significant effects on the concentrations of each of the minerals in the earlier studies referred to.

Two sets of correlations are presented, (1) those attributable to the effects of all or some of the factors listed above (referred to as 'correlations of effects') and (2) those remaining when the effects of the specified factors have been removed as sources of variation in mineral concentration. These 'residual correlations' correspond to those in a group of sheep of the same breed, age, lambing performance, week of lambing and so on. Correlations of effects are presented for three situations (*a*) correlations arising when all the factors listed above were included in the model (the residual correlations were also derived from this model), (*b*) correlations arising from differences in mineral concentrations among breeds, and (*c*) correlations arising from differences in mineral concentrations among age classes. Correlations attributable to breed and age were calculated from the sums of squares and products attributable to each when fitted subsequently to all the other factors. For each simple correlation a corresponding partial correlation is also given, the latter implying the correlation of any two variables (i.e. two mineral concentrations, or one mineral and live weight) when the values of the other minerals were held constant. Corresponding partial correlations are not given for the simple correlations attributable to the effects of breed or age because of the small number of breed or age classes involved.

RESULTS

Correlations among mineral concentrations attributable to the combined effects of breed, inbreeding, age, number of lambs born, week of lambing and swayback history are shown in Table 1. The highest correlations were found between P and Ca concentrations and between P and Cu concentrations (−0·65 and −0·54 respectively). Other associations too large to be ignored were between the concentrations of Mg and K, Na and Cl, and Ca and K. In all these cases except the last the partial correlation was as high as the simple, suggesting that the correlation between the two minerals did not arise from a common relationship with any of the other five minerals.

In view of the small number of degrees of freedom between breeds (4 D.F.) and ages (3 D.F.) only the highest of the correlations shown in Table 1 seem worth considering. They suggest that breed differences in Ca concentration were positively related to breed differences in Cu concentration and negatively related to those in P level, whilst Cu and P were also negatively correlated. Among the correlations related to changes with age, that between Ca and Mg concentrations (0·97) was the highest, followed by that between Cu and K (−0·9[illegible]). Others which appeared to be too large to be ignored ($P < 0·1$) are indicated in the table.

Residual correlations are shown in Table [illegible]. Seven of the twenty-one simple correlations are statistically significant but all are small (< 0·2). The partial correlations were again very similar in magnitude to the simple ones. The absence of residual correlation between Ca and P concentrations contrasts with the apparently high correlation of these minerals attributable to the effects of specific factors. Similarly there was no significant residual correlation between Ca and K concentrations although both changed with age.

Table 4 shows a variety of correlations of mineral concentrations with live weight of the animal (about 7 months previously). The correlations attributable to changes with age are not surprising, since the concentrations of several of the minerals were shown earlier to change with age (Field, Wiener & Wood, 1969) and live weight is known to increase over the age range studied (Wiener, 1967). Correlations with live weight

Table 1. *Correlations among mineral concentrations‡ attributable to the effects of all the factors included in the statistical model (see text)*

Simple correlations (18 D.F.) below and partial correlations (13 D.F.) above the diagonal.

Mineral	Ca	P	Mg	K	Na	Cl	Cu
Ca	—	−0·69**	0·28	0·20	0·00	0·21	−0·31
P	−0·65**	—	0·38	−0·11	−0·01	0·02	−0·61*
Mg	0·26	0·11	—	0·46†	−0·20	0·25	0·20
K	0·39†	−0·10	0·46*	—	0·43	−0·43	−0·22
Na	0·29	−0·18	0·10	0·35	—	0·50†	−0·04
Cl	0·29	−0·24	0·14	−0·13	0·41†	—	0·15
Cu	0·14	−0·54*	−0·09	−0·24	−0·01	0·27	—

Significance of correlations, †$P < 0·1$, * $P < 0·05$; ** $P < 0·01$.
‡ Concentrations in whole blood for P and Cu, in plasma for other minerals.

Table 2. *Simple correlations among mineral concentrations‡ attributable to the effects of six breed (below diagonal) and of five ages (above diagonal)*

Mineral	Ca	P	Mg	K	Na	Cl	Cu
Ca	—	−0·79	0·97**	0·84†	−0·17	−0·63	−0·69
P	−0·81†	—	−0·83†	−0·83†	−0·06	0·68	0·62
Mg	−0·12	0·49	—	0·79	−0·02	−0·49	−0·67
K	0·49	−0·22	0·35	—	0·17	−0·83†	−0·92*
Na	0·57	−0·46	0·14	0·65	—	0·23	−0·46
Cl	0·39	−0·39	0·40	0·74	0·76	—	0·63
Cu	0·83*	−0·95**	−0·29	0·41	0·71	0·62	—

Significance of correlations, † $P < 0{\cdot}1$; * $P < 0{\cdot}05$; ** $P < 0{\cdot}01$.
‡ Concentration in whole blood for P and Cu, in plasma for other minerals.

Table 3. *Residual correlations among mineral concentrations‡ when the effects of a variety of factors have been removed as sources of variation (see text)*

Simple correlations (304 D.F.) below and partial correlations (299 D.F.) above the diagonal.

Mineral	Ca	P	Mg	K	Na	Cl	Cu
Ca	—	−0·03	0·06	0·20***	0·14*	−0·07	0·17**
P	0·01	—	0·16*	0·10	0·01	−0·15*	−0·00
Mg	0·08	0·16**	—	0·06	−0·01	0·11*	0·08
K	0·19***	0·09	0·10	—	−0·05	0·18**	−0·01
Na	0·13*	−0·00	0·01	−0·01	—	0 08	−0·01
Cl	−0·04	−0·12*	0·09	0·16**	0·06	—	−0·11*
Cu	0·18**	0·02	0·08	0·01	0·01	−0·12*	—

Significance of correlations, * $P < 0{\cdot}05$; ** $P < 0{\cdot}01$; *** $P < 0{\cdot}001$.
‡ Concentrations in whole blood for P and Cu, in plasma for other minerals.

Table 4. *Correlations of mineral concentrations with live weight*

	Correlation attributable to the effects of all factors		Simple correlations attributable to the effects of		Residual correlations	
Mineral	Simple	Partial	Breed	Age	Simple	Partial
Ca	−0·21	0·17	−0·64	−0·91*	0·11*	0·09
P	0·33	0·16	0·61	0·93	−0·04	−0·05
Mg	−0·42†	−0·43	−0·14	−0·95*	0·13*	0·12*
K	−0·33	−0·42	−0·39	−0·74	−0·01	−0·05
Na	0·06	0·24	−0·08	0·09	0·05	0·04
Cl	−0·00	0·08	−0·46	0·51	0·05	0·05
Cu	−0·51*	−0·57*	−0·57	0·54	0·11*	0·09

Significance of correlations, † $P < 0{\cdot}1$; * $P < 0{\cdot}05$.

within sub-classes (residual) were all very low, but were significant ($P < 0{\cdot}05$) for Ca, Mg and Cu. Only in the case of Mg was the corresponding partial correlation also significant.

DISCUSSION

The results suggest that at least some of the factors considered in the analysis produced correlated changes in the concentrations of some of the minerals. In a number of cases the correlations arising from breed differences and those arising from age differences tended to cancel each other (e.g. Cu, Ca and Cu.P) whilst in other cases the correlations tended to reinforce each other (e.g. Ca.P and Mg.K).

An inverse relationship between Ca and P derived from a comparison of normal and deficient animals has been suggested by a number of workers (quoted by Stewart, 1934 and Underwood, 1966).

However, for a control group of sheep Stewart (1934) reported large fluctuations within the normal range without a corresponding inverse fluctuation in the other mineral. The analogy may be drawn with the negative correlation between Ca and P attributable to breed and age differences (Table 2), or 'effects' in general (Table 1) and the virtual absence of a correlation within subclasses.

Except in relation to age changes, we have found no evidence of an association between Ca and Mg concentrations in blood plasma in clinically normal sheep.

The specified factors in the present analysis accounted for only a small proportion of the total variation for Na, K, and Cl (5–9 %), little more for Ca and P (12–15 %) and still not a large proportion for Cu (27 %) and Mg (35 %). Yet shorn of this variation, the residual correlations were all small and suggest that for many purposes the concentrations of the seven minerals can be treated as virtually independent. Even the highest of these residual correlations (0·20) implies that 96 % of the residual variation of one mineral was independent of the variation in the other mineral. For other purposes, however, the small but significant correlations suggest physiological relationships which may be of interest. There is nothing in these data, however, to correspond to the relationship in whole blood of K and Na where sheep with the gene for a high concentration of K have a low concentration of Na and vice versa (Evans & King, 1955). Within each genetic type, however, the variation of whole blood K and Na may not be correlated (Kidwell, Bohman, Wade, Haverland & Hunter, 1959). The concentrations of all the minerals studied in this paper showed a continuous distribution with no suggestion of bimodality.

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Breed, Bodyweight and Age as Factors in the Mortality Rate of Sheep following Copper Injection

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SUMMARY.—In a flock comprising three breeds and their crosses, 17 deaths occurred following a prophylactic, subcutaneous injection of a standard dose of 50 mg. of copper calcium edetate (1·04 per cent. of the 1,629 sheep injected over a five-year period). All but one of the deaths occurred within 72 hours of injection. Mortality rate increased steadily with decreasing liveweight of sheep. Deaths occurred among sheep from 37 to 104 lb. liveweight and none among heavier sheep. Among the lighter sheep (below 100 or 120 lb. liveweight), however, there was a significant breed difference in mortality. For the whole flock, mortality rates (per cent.) for the six breed types involved were: Scottish Blackface 0·52, Cheviot 0·00, Blackface-Cheviot 0·00, Welsh 2·73, Welsh-Cheviot 0·32, Welsh-Blackface 2·15. The highest incidence was thus associated with the Welsh genotype and the lowest with the Cheviot genotype. There was a tendency for mortality to decline with increasing age of sheep.

Introduction

DEATHS FOLLOWING injection of copper as copper calcium edetate have been reported for lambs by Allcroft, Buntain and Rowland (1965), and for adult sheep by Ishmael, Howell and Treeby (1969), Ishmael, Treeby and Howell (1970) and by Wiener and Field (1970). In the present paper the data briefly referred to by Wiener and Field (1970), in the context of genetic variation in copper metabolism, are supplemented and described in greater detail.

Material and Methods

The flock of about 340 breeding ewes, in regular ages up to five-and-a-half years old, is part of a long-term breeding experiment. It comprises the Scottish Blackface, South Country Cheviot and Welsh Mountain breeds and the crosses, bred *inter se*, among these breeds. Sheep of all three breeds and of the three crossbred types are maintained at different levels of inbreeding from 0 per cent. to 50 per cent. The sheep are kept together as a single unit in fields of sown pastures at Blythbank, Peeblesshire. The flock has been self-contained as a breeding group on the female side since 1955 and on the male side since 1958. More details of the flock were given by Wiener, Field and Wood (1969).

Subcutaneous injections of 50 mg. copper as a commercial preparation of copper calcium edetate have been given to ewes in this flock during mid-pregnancy (between January and March) each year since 1965. Injections had been indicated by the occurrence of swayback in this flock in 1964, when 15 per cent. of lambs were affected following isolated cases in previous years, and by confirmation of the low blood copper status of the flock in February, 1965 (Wiener & Field, 1966).

Results

Four deaths were recorded within 72 hours of the injections in 1965 and 11 in 1969. These were examined *post mortem*. The lesions were compatible with those found in acute copper poisoning following parenteral administration of copper (Macleod & Watt, 1970). In 1967 also, two sheep died within 48 hours of injection from suspected copper poisoning but no *post-mortem* examinations were carried out.

The incidence of death differed significantly ($P<0.01$) among the breeds. Assuming that all sheep were subject to equal risk, more sheep died, compared with expectation, from among the Welsh and the Welsh-Blackface crossbreds and fewer from among the rest, particularly the Cheviot and Cheviot crosses. Table I shows the numbers.

In addition to the 17 deaths directly attributed to the copper injection, nine other sheep died between three days and four weeks after injection. At the time, the injection was not thought of as a contributory factor in these deaths and *post-mortem* examinations were not made. However, on the basis of the one confirmed copper poisoning case three-and-a-half weeks after injection in 1969, the other deaths might be relevant in the present context. They are shown in the last column of Table I and their distribution reinforces the breed differences already noted.

The sheep in this flock were very variable in liveweight with the breed, inbreeding and age as major factors contributing to this variation in addition to individual variation. Risks were clearly related to the dose of copper per unit weight of sheep, but breed differences in mortality were still significant ($P<0.05$) when confined to sheep below 100 lb. (or 120 lb.) liveweight. The distributions are shown in Table II. The lightest sheep to die weighed 37 lb. and the heaviest 104 lb. at the date of injection.

Mortality tended to decline with increasing age (Table III), but the probability was 1 in 10 that the differences between the age classes in the numbers dying was due only to chance. The continuous decline in mortality from the youngest to the oldest class is, however, more significant ($P<0.05$). Each breed was proportionately represented in each age class.

Concentrations of copper in the livers varied from 107 to 357 p.p.m. DM (average 192) for the 11 sheep examined in 1969 and from 239 to 324 p.p.m. DM (average 274) for the four sheep in 1965. There

TABLE I
BREED DISTRIBUTION OF SHEEP INJECTED WITH COPPER AND DYING AS A CONSEQUENCE AND OTHER DEATHS WITHIN FOUR WEEKS OF INJECTION (1965-1969)

	Number injected	Deaths attributed to injection			Other deaths†
		Observed		Expected* number	
		Number	Per cent.		
Scottish Blackface	193	1‡	0·52	2·0	1
Cheviot	162	0	0·00	1·7	0
Blackface-Cheviot crossbred	324	0	0·00	3·4	1
Welsh Mountain	220	6	2·73	2·3	3
Welsh-Cheviot crossbred	311	1	0·32	3·2	1
Welsh-Blackface crossbred	419	9‡	2·15	4·4	3
All sheep	1,629	17‡	1·04	17·0	9

* Expectation if all sheep subject to equal risk
† No *post-mortem* examinations (see text)
‡Including one sheep not examined *post-mortem* (i.e. two of total 17).

TABLE II
LIVEWEIGHTS OF SHEEP, BY BREED, INJECTED WITH COPPER AND, IN PARENTHESIS, NUMBERS DYING AS A CONSEQUENCE

	Liveweight (lb.)								Average live-weight
	<40	40—59	60—79	80—99	100—119	120—139	140—159	160 >	
Blackface	0	2	12	39	62 (1)	48	23	7	115
Cheviot	0	2	19	34	50	41	11	5	110
Blackface × Cheviot	0	0	19	75	85	69	44	32	118
Welsh	2 (1)	20 (3)	81 (1)	78 (1)	33	6	0	0	82
Welsh × Cheviot	0	5	58 (1)	102	80	58	8	0	99
Welsh × Blackface	0	12 (4)	74 (2)	132 (3)	129	63	8	1	99
Total no injected	2	41	263	460	439	285	94	45	
Deaths:									
No.	1	7	4	4	1	0	0	0	
Percentage	50·0	17·1	1·5	0·9	0·2	0	0	0	

were no clear differences associated with breed or age of ewe.

Discussion

A standard dose of 50 mg. copper as copper calcium edetate (manufacturer's recommended dose) was administered per sheep. Thus, the dose per 1 lb. liveweight of sheep varied, at the extremes in this flock between approximately 0.3 and 1.2 mg. This appears to have been an important factor in the risks of death. Sutherland, Moule and Harvey (1955) have also noted an association of death rate and dosage using copper glycinate. However, apparently superimposed is a genetic difference which makes some breeds, and perhaps some sheep, more susceptible to this form of copper poisoning, or others more resistant. Stated conversely, the breed differences in mortality following copper injection are not fully accounted for by breed differences in bodyweight.

In 1964, the incidence of swayback in this flock was found to have been markedly influenced by the breeding of the sheep even after making allowance for the differences in the liveweight of the animals (Wiener, 1966; Wiener & Sampford, 1969). The Welsh genotype was then associated with the lowest incidence of swayback, and now with the highest

TABLE III
AGE DISTRIBUTION OF SHEEP INJECTED WITH COPPER AND NUMBERS DYING AS A CONSEQUENCE

	Age (years)			
	2	3	4	5+
Number injected	458	401	398	372
Deaths: No.	8	5	4	0
Percentage	1·75	1·25	1·0	0

mortality following copper injection. For the other two breeds, Cheviot and Blackface, the manifestation of copper deficiency, through swayback, and deaths from excess of copper are not so apparently opposite sides of the same coin. The Cheviot genotype was associated with only one death (a Cheviot-Welsh sheep) following injection, while in swayback incidence it was intermediate between the Welsh and the Blackface. The Blackface genotype was associated with the highest incidence of swayback, but with an intermediate mortality rate following copper injection (on account of the relatively high losses among the Blackface-Welsh crosses). The mortality rates among the crossbred sheep suggest, however, that genic interactions could be involved, although the data are too scanty to choose among alternative genetic hypotheses.

Genetic differences have also been reported for

sheep in this flock in the concentrations of copper in their blood (Wiener, Field & Wood, 1969) and livers (Wiener & Field, 1969b). If genetic variation in copper levels affects the risks from copper injection, and higher levels increase the risks, the Welsh and Welsh crosses conformed to expectation since they had the highest average blood copper levels and suffered the most deaths following injections. On this basis, however, some deaths might also have been expected among the Blackface-Cheviot crosses, yet there were none. This may be due to chance since the numbers involved are very small, but it is of interest that this group was on average the heaviest of those involved and hence received the lowest dose of copper per unit liveweight. The relationship of deaths with the reported breed variation in liver copper concentration is more tenuous, but perhaps not surprisingly so since the liver copper concentrations of the sheep which died were not at toxic levels.

In former years ewes of the youngest age class in this flock had a lower copper concentration in their blood than did older sheep (Wiener & Field, 1966; Wiener, Field & Wood, 1969), but mortality following copper injection was, in fact, slightly greater in this young class. Unpublished results from a sample of the flock bled in February, 1969, after the injections also suggested lower blood copper concentrations for the youngest age class. Evidently, therefore, any protection against copper poisoning expected from the presumed lower copper status was offset by other factors, possibly the, on average, lighter weight of the younger sheep. Ishmael, Howell and Treeby (1969) have also noted a tendency for mortality following injection to be slightly higher among the younger sheep.

The mortality rate following copper injection differed significantly ($P<0.001$) in the five years studied—from none in two of the years to 11 in 1969. Ishmael, Howell and Treeby (1969) have reported that farm to farm variation in mortality appears to exist. It seems possible, therefore, that a clinical manifestation of genetic variation in the response to too much (or too little) copper depends on a threshold which varies from year to year and from farm to farm.

Information from the present experimental flock can be used to examine the possibility that this threshold might be associated with year to year differences in the weight of the sheep. In this flock liveweight of the sheep has been declining over the years. This, however, can be associated with an increasing level of inbreeding. Any normal seasonal variation in weight is superimposed. In 1969, when most deaths occurred, average weights of the sheep were slightly lower than in any of the previous four years. 1965, however, provides contradictory evidence with the greatest average weights associated with four deaths. Examination of weather records showed no clear relationship with year differences in mortality rate. In 1969, in the days immediately following the injection, temperatures were continuously below freezing point and there was a strong easterly wind. In the other years, however, the weather was less harsh but deaths occurred in two of them.

Following the deaths in 1969, 48 sheep which had not been injected, because they were presumed to be less than about six weeks pregnant, were bled a week later. Blood copper levels indicated a higher average level than anticipated (83 μg. per 100 ml.) with individual variation from 32 μg. per 100 ml. to 136 μg. per 100 ml. Statistical analysis showed that genetic and other factors influencing copper levels conformed to the established pattern (Wiener, Field & Wood, 1969).

While the sheep in this flock might not have received a copper injection had the blood levels of February, 1969, been known in advance, it is common practice to treat a flock, as here, on the evidence of its history of swayback. This had affected all breeds and crosses in this flock, except the Welsh, to a greater or lesser extent. Moreover, all the breeds in this flock (including the Welsh) were thought, on the basis of blood samples in former years, to be low in copper status, although the levels had differed among the breeds. Clearly the evidence of former years was not an adequate basis for a decision to administer copper. Genetic variation in copper concentrations in the blood of sheep, particularly if it were found to be important within breeds as it has been among breeds, leads to the further complication that a small number of randomly picked sheep may not adequately represent the copper status of a large flock.

However, in relation to the risks of death following copper injection it appears likely that even with the presumption of a low copper status for a flock of sheep, the precise dose of copper per sheep may be more critical than the usual recommendations of a standard dose imply. The weight of the sheep appears to be a crucial factor.

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Résumé

Dans un troupeau comprenant trois races et leurs issues, 17 morts ont suivi l'injection sous-cutanée prophylactique d'une dose standard de 50 mg. de cuivre sous forme de calcium de cuivre edétate (1,04 pour cent des 1.629 moutons injectés dans

une période de cinq ans). A une exception près, toutes les morts sont survenues dans les 72 heures après l'injection. Le taux de mortalité augmentait en proportion décroissante du poids des moutons. Les morts sont survenues parmi les moutons pesant de 16,8 à 47,2 kg. sur pied, et pas du tout chez les moutons plus lourds. Parmi les moutons de petite taille (de moins de 45 à 54 kg. sur pied), cependant, il y avait une différence significative dans le taux de mortalité par rapport au type de race. Dans la totalité du troupeau, les taux de mortalité (pour cent) pour les six types de races étaient: Scottish Blackface 0,52, Cheviot 0.00, Blackface-Cheviot 0.00, Welsh 2.73, Welsh-Cheviot 0,32, Welsh-Blackface 2,15. La plus haute incidence est donc associée avec le génotype Welsh et la plus basse avec le génotype Cheviot. La mortalité a tendance à décroître en proportion inverse de l'âge du mouton.

Zusammenfassung

In einer aus drei Rassen und ihren Kreuzungen bestehenden Schafherde ereigneten sich nach einer prophylaktischen Subkutaninjektion der üblichen Dosis von 50 mg. Kupfer, in Form von Kupfer-Kalzium Athylen-Diamin-Tetrazetat, 17 Todesfälle (1,04 prozent von den im Laufe von fünf Jahren behandelten 1.629 Schafen). Mit einer einzigen Ausnahme starben sämtliche Schafe innerhalb von 72 Stunden nach der Injektion. Die Zahl der Todesfälle nahm mit abnehmendem Körpergewicht der Schafe zu, und somit waren Schafe mit einem Gewicht von 16,8 kg. bis 47,2 kg. betroffen, jedoch nicht oberhalb dieser Grenze. Zwischen den leichteren Schafen (unter 45 bzw. 54 kg. Lebendgewicht) bestand allerdings ein bedeutsamer Unterschied in der Sterblichkeit. Der Prozentsatz der Todesfälle bei den einzelnen Rassen des Bestandes betrug: Schottisches Schwarzkopfschaf 0,52, Cheviot 0,00, Schwarzkopfschaf × Cheviot 0,00, Walisisches Schaf 2,73, Walisisch × Cheviot 0,32, Walisisch × Schwarzkopfschaf 2,15. Die höchsten Sterblichkeitsziffern betrafen somit den walisischen Genotyp und die niedrigsten den Cheviot-Genotyp. Mit zunehmendem Alter der Tiere war eine abhenmende Neigung zum tödlichen Ausgang zu verzeichnen.

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9

The concentration of minerals in the blood of genetically diverse groups of sheep

IV. Factors influencing seasonal changes in copper concentration

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SUMMARY

Changes in the concentration of copper in the blood of 241 adult ewes bled 4 times over a 12-month period (and 332 ewes over a shorter period) were analysed to examine sources of variation in the changes. Breed, age and swayback history were the most significant of the factors associated with both the amount and rate of decline in copper level from summer through autumn to winter. The number of lambs born, age of ewe, and swayback history were the most significant factors associated with the increase in levels from winter to the following summer.

There was a tendency for the classes of sheep with the relatively higher concentrations of copper in their blood to show less seasonal fluctuation in those levels than classes of sheep with relatively lower concentrations of copper.

INTRODUCTION

The concentration of copper in the blood of a enetically diverse flock of sheep was shown in a revious paper (Wiener, Field and Wood, 1969) o have been affected by the breed, by cross- reeding, by the previous swayback history of the neep and by other factors such as the age, live eight and lambing performance of the ewes. The neep had been bled on a number of occasions over n 18-month period and visual inspection of the sults gave an impression that the amount of ange from one time to the next was not the same r all classes of sheep. This seemed to be most pparent when the amount of change was expressed a ratio of the level at the start instead of being pressed as a difference. The physiological con- quences of a fall or a rise in copper concentration ay be quite different depending on the level at the ginning. The present paper gives the results of a ler statistical analysis of these changes in copper ncentration in the blood. In a statistical sense, interactions of a variety of factors with season the year have become main effects.

MATERIALS AND METHODS

The animals, the flock management, and the blood sampling procedures were described in detail by Wiener *et al.* (1969). Briefly, the flock comprises sheep of the Scottish Blackface, Cheviot and Welsh Mountain breeds and the crosses (F_2) made between these breeds. Additionally, comparisons were made at various levels of inbreeding (from 0 to 50 %) of both purebred and crossbred sheep. There were five age classes and other classifications include those associated with lambing performance of the sheep. Twenty ewes which had produced swayback lambs in 1964 remained in the flock and they are compared with their contemporaries which produced normal lambs in the same year.

The essential feature of flock management was that there has been no subdivision of the flock associated with the breeding of the animals. The flock has been self-contained on the female side since 1955, and on the male side since 1958.

In February 1965, and again in February 1966, the ewes, but not the young unmated females, were

injected with 50 mg of copper (as copper calcium edetate).

Changes in copper concentrations have been analysed among the following four occasions when the sheep were bled: (1) May or June 1965 (the sheep were bled in groups 6 weeks after lambing); (2) 19–20 October 1965; (3) 31 January 1966—1 day prior to copper injection; (4) 7 June 1966. These occasions will be referred to as summer (1965), October, January and June respectively. A total of 241 ewes were present on all these four occasions, and 332 on each of the last three occasions (in October of each year a group of 18-month-old females, previously unmated, is taken into the breeding flock and the oldest age class of ewes is discarded). The full process of statistical analysis as described in the next section was carried out for both sets of animals.

Statistical analysis

The change in copper concentration between any two blood-sampling occasions was calculated for each individual sheep, both for the change in the absolute values (μg/100 ml whole blood) and for the change in these values after their conversion to logarithms. For the 241 animals present on all four occasions this yielded estimates of six differences in both absolute and log units, and for the 332 present on three occasions, three such sets of differences were obtained. Analysis of the differences consisted of fitting a linear model of parameters representing the effects of breed, live weight of ewe, swayback history, inbreeding, various aspects of lambing performance and the age of the ewe, as described in the earlier paper referred to above. Differences among a set of parameters representing, for example, breeds, therefore, are estimates of differences between animals which are alike in respect of all other parameters fitted; that is, animals which have the same number of lambs, same swayback status, same age, etc. A number of interactions were also fitted. Parameters were excluded on the criteria of significance as outlined in the previous paper. The parameters retained in the final model are shown in Table 1.

A complication in the analysis, not met with previously, arose from the fact that particular factors may have significant effects at one occasion in time but not at another. For example, copper concentration in the summer of 1965 might be affected by lambing performance in that year, but not by the lambing performance in the subsequent year. At the same time the concentration of copper in the blood in 1966 might be affected by lambing performance in that year, but might be thought less likely to have been affected by the lambing performance in the preceding year. In the analysis

Table 1. *Significance* of various factors† on the difference in copper concentration between bleedings in summer* 1965, *October* 1965, *January* 1966, *and June* 1966

Results from analyses of changes in absolute Cu values and changes in log Cu values.

	241 ewes present on all four occasions												332 ewes present on each of last three occasions					
	Summer–Oct.		Summer–Jan.		Summer–June		Oct.–Jan.		Oct.–June		Jan.–June		Oct.–Jan.		Oct.–June		Jan.–June	
	Abs.	Log.	Abs.	Log.	Abs.	Log.	Abs.	Log.	Abs.	Log.	Abs.	Log.	Abs.	Log.	Abs.	Log.	Abs.	Log.
Breed	5	1	20	0·1	N.S.	1	5	10	20	N.S.	N.S.	N.S.	0·1	5	20	N.S.	20	N.S.
Swayback history	20	10	10	5	N.S.	N.S.	N.S.	20	20	N.S.	10	5	N.S.	20	20	20	10	5
Mature *v.* immature	.	.	.	.	.	.	.	.	.	.	.	.	5	0·1	10	N.S.	0·1	0·1
Age within mature	N.S.	N.S.	0·1	1	5	10	1	0·1	N.S.	N.S.	5	10	1	0·1	N.S.	N.S.	N.S.	N.S.
No. of lambs, 1965	N.S.	N.S.	N.S.	N.S.	20	N.S.	N.S.	N.S.	5	5	5	1	N.S.	N.S.	5	5	5	5
No. of lambs, 1966	N.S.	20	N.S.	N.S.	10	20	N.S.	N.S.	1	1	5	1	N.S.	N.S.	5	1	5	1
Week of birth, 1965	5	5	1	1	5	10	N.S.	N.S.	N.S.	20	N.S.	20	N.S.	N.S.	N.S.	10	N.S.	10
Week of birth, 1966	N.S.	N.S.	20	10	0·1	0·1	N.S.	N.S.	0·1	0·1	0·1	1	N.S.	N.S.	0·1	0·1	0·1	1
Place of inbreeding	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	10	10	N.S.	N.S.

* The numbers in the body of the table represent percentage probability levels (*N.S.* represents $P > 20$ %).

† Interactions (fitted in the model) are not shown in the table.

of changes in copper concentration it was considered more important to apply a common statistical model to both the start and end-point of any period of change (even at the risk of including some parameters which might be excluded on logical grounds) than to run the risk of complications arising from changes in the statistical model between start and end-point. The criterion adopted in the analysis of change in concentration was to include those parameters which had been found to have had some importance at least on one of the occasions.

RESULTS

The parameters included in the final model of the analysis and their significance as sources of variation are shown in Table 1. Clearly, three of the six changes in copper concentrations among sheep

Table 2. *Effects of breed, swayback history, age of ewe and number of lambs on changes in the concentration of copper (second concentration minus first) in whole blood (μg/100 ml)*

Values (when all other parameters were held constant) are shown as deviations from the average and are based on 241 ewes (except where otherwise indicated). Within each group of parameters (e.g. breed) values in a column suffixed with the same letter differ significantly ($P < 0.05$).

	No. of ewes in the deviating class	Interval between bleedings*			
		Summer–Oct.	Oct.–Jan.	Total Summer–Jan.	Jan.–June
Average change ...	.	−13·1	−16·1	−29·2	+23·4
Breed:					
Blackface	27	−13·9a	+3·7a	−10·2ab	−1·7
Cheviot	24	+0·9	−0·3	+0·6	+3·2
Welsh	30	+16·1abcd	−8·3ab	+7·8a	−2·2
Blackface × Cheviot	46	−2·6b	+7·9bcd	+5·4b	−2·1
Blackface × Welsh	62	−1·6c	−0·4c	−2·0	+0·1
Cheviot × Welsh	52	+1·1d	−2·6d	−1·6	+2·7
Ewes with swayback lambs in 1964 as a deviation from ewes with normal lambs	20	−11·6	−1·1	−12·7	+9·6
Age†					
Ewes born in 1964 as a deviation from ewes born earlier	90		−11·8bde		+21·3abc
Deviation of ewes born before 1964 from their average (year of birth)					
1963	74	−7·4	−8·1ac	−8·0ab	+4·7
1962	61	+3·7	−1·4e	−1·9	+2·7c
1961	82	+3·1	+4·2cd	+3·9b	−1·8b
1960	24	+0·6	+5·3ab	+5·9a	−5·6a
No. of lambs born in 1965					
Barren ewes as a deviation from ewes with lambs	22	+6·4	−0·8	+5·7	−14·3
Ewes with 1 lamb as a deviation from average‡	107	+3·5	−1·1	+2·5	+0·5
No. of lambs born in 1966					
Barren ewes as a deviation from ewes with lambs	20	−2·1	+2·0	−0·1	+16·2
Ewes with 1 lamb as a deviation from average‡	102	−1·1	+2·8	+1·4	+0·2

* Bleedings in the summer of 1965 (6 weeks after parturition), on 19–20 October 1965, 31 January 1966 and June 1966. Ewes were injected with copper on 1 February 1966.

† Age effects shown for the period from October to January and from January to June are based on 332 ewes ncluding young sheep entering the flock in October 1965). There were two more ewes among the older ones than ie numbers shown.

‡ The deviation for ewes with twins or triplets takes the same value with the opposite sign.

bled four times can be deduced given the others (and one of the three changes for sheep bled three times). The statistical significance, however, cannot be similarly deduced. Whilst Table 1 shows the results of all possible changes, presentation will be restricted in later Tables.

In most respects the results from the 241 sheep which were present on all occasions are closely paralleled by the results from the 332 sheep present on the last three occasions. This suggests that, except in terms of age, the young females which entered the flock in October were typical of the remainder. However, standard errors attached to the regression coefficients were in general lower when derived from the larger number (332) of animals. In consequence some of the effects which failed to reach significance in the analysis of 241 were statistically significant on the basis of 332 and a few others appeared to become more highly significant. This is apparent from Table

It can also be seen in Table 1 that effects often statistically more significant when based the analysis of logarithms—that is to say, changes were expressed as ratios instead of ferences. There were, however, some exceptions

More detailed consideration will now be g to the effects of related parameters grou together for convenience. The values shown further Tables are those when all other p meters in the analysis were held constant. E due to week of birth and those due to inbreed are not detailed in Tables 2 and 3.

Table 3. *Percentage effects of breed, swayback history, age of ewe and number of lambs on changes in the concentration of copper in whole blood*

The second concentration was expressed as a percentage of the first following analysis of the changes in the log Cu values. Values (when all other parameters were held constant) are shown as deviations from the average and are based on 241 ewes (except where otherwise indicated). Within each group of parameters (e.g. breed) values in a column suffixed with the same letter differ significantly ($P < 0.05$). Values for any individual class cannot be added to values for any other class (except the average) to obtain combinations (see text).

	Interval between bleedings*			
	Summer–Oct.	Oct.–Jan.	Total Summer–Jan.	Jan.–Ju
Average change ...	−19·6	−23·7	−38·7	+42·7
Breed:				
Blackface	−21·0abcde	−5·9a	−19·5abcd	+18·3
Cheviot	−1·3af	−3·1b	−3·5	+5·0
Welsh	+22·3bfgh	−2·9c	+14·0a	−13·2
Blackface × Cheviot	−1·7cg	+11·9abcde	+8·2b	−10·
Blackface × Welsh	−0·7dh	0·0d	−0·4c	+5·
Cheviot × Welsh	+8·8e	+1·0e	+7·7d	−2·
Ewes with swayback lambs in 1964 as a deviation from ewes with normal lambs	−15·1	−8·5	−17·0	+40·1
Age†				
Ewes born in 1964 as a deviation from ewes born earlier	.	−20·1bdf	.	+81·6b
Deviation of ewes born before 1964 from their average (year of birth)				
1963	−4·4	−11·5ace	−13·4abc	+15·2
1962	+0·7	+0·0ef	+0·3c	+7·6
1961	+2·7	+5·1cd	+6·5b	−4·7
1960	+1·3	+8·1ab	+9·3a	−16·0
No. of lambs born in 1965				
Barren ewes as a deviation from ewes with lambs	+11·4	+6·7	+14·9	−39·1
Deviation from average of ewes with 1 lamb‡	+1·3	−1·9	−0·6	+4·1
No. of lambs born in 1966				
Barren ewes as a deviation from ewes with lambs	−14·7	−1·4	−2·1	+67·4
Deviation from average of ewes with 1 lamb‡	−2·5	+0·5	−1·5	+6·1

*, †, ‡ See Table 2.

Table 2 shows the results of an analysis of the absolute changes in copper levels and Table 3 the results after transforming individual values to logarithms. For ease of appraisal, however, the results of the logarithmic analysis have been converted into percentage changes. The copper level at the end of any period was expressed as a percentage of that at the beginning and the difference between the two is shown. The sign (in Tables 2 and 3) indicates the direction of the change, i.e. a negative sign implies that the value at the end of the period is lower than that at the beginning. A disadvantage of the presentation in Table 3 is that the separate deviations from the average changes are no longer additive.

Breed

The absolute changes of the copper levels are shown in Table 2. For example, from Table 2 it can be seen that copper levels fell on average by 13·1 μg/100 ml blood between summer 1965 and October of that year. Copper levels of sheep of the Blackface breed fell by 13·9 μg more than this average (i.e. by a total of 27 μg) whilst that of Welsh sheep fell by 16·1 μg less than this (in other words their Cu levels increased by 3 μg between the summer and October).

Logarithmic analysis (shown in Table 3) yielded the answer that, on average, October levels were 19·6 % below those in the summer whilst, for example, for Blackface alone the corresponding figure was 40·6 % (i.e. 21 % more than average), for Welsh 2·7 % above summer level (i.e. a fall of 22·3 % less than average), and so on.

Relative to the copper values in the summer of 1965, the breed effects were on average more highly significant when changes were expressed as ratios (i.e. on the logarithmic scale). A major component of the breed effect arose from the difference between the Blackface and the Welsh. The Blackface fell most in copper level and the Welsh least between the summer and October, and also over the total period from the summer to the following January. The recovery of copper levels between January and June 1966 was not very different for any of the breeds, although relative to the January level the change in the Blackface was again, expectedly, the greatest and that of the Welsh the least.

On average, the Blackface–Cheviot crossbred sheep fluctuated less in copper level than the average of the Blackface and Cheviot purebreds. They fell less in periods of decline and increased less in the period of recovery. This effect was sufficient to make the average changes of all three crosses less than the average changes of all three pure breeds.

Swayback

Twenty ewes had remained in the flock from among those producing swayback lambs in 1964. The ewes comprised 9 Blackface, 1 Cheviot, 6 Blackface × Cheviot, 2 Blackface × Welsh and 1 Cheviot × Welsh. These numbers were considered too few for a separate analysis by breed of seasonal changes of swayback-producing ewes. When breed effects were held constant copper levels of these ewes fell more than the average for normal ewes between the summer and the following January (12·7 μg/100 ml, or 17·0 %) with most of that above-average fall having occurred by October. The corresponding increase from January to June was also greater than average. Large standard errors, associated with the small number of ewes in this class, have allowed only the total decline and the subsequent rise in copper level to reach statistical significance ($P < 0{\cdot}05$) when analysed on the log scale.

Age of ewes

There was a marked tendency for the copper level of younger ewes to decline more than that of the older sheep over the autumn and winter period, but particularly from October to January. From January to June the copper levels of the young sheep increased much more sharply than those of older sheep. The young, previously unmated, sheep entering the breeding flock for the first time in October 1965 showed particularly marked changes.

Number of lambs

The copper concentrations of ewes which failed to have lambs in 1965 appeared to fall less between the summer of 1965 and October, and again over winter, than the levels of ewes with lambs. Ewes with single lambs showed a lesser fall than the ewes with twins. The corresponding increase from January to June (and from October to June) was smaller for ewes which had been barren in 1965 than ewes with lambs, and less for those which had had singles than for those that had had twins. Statistically, only the different amounts, or rates, of increase in copper concentration from January to June (and October to June) were significant (see Table 1).

In relation to the number of lambs born in 1966, the increase in copper concentration between January and June (and between October and June) was significantly affected by the number of lambs born in 1966 (Table 1). The direction of these effects however was the opposite to that noted in relation to number of lambs born in the previous year. Ewes with twins had the smallest increase in copper concentration (approx. 7 μg/100 ml between January and June) and barren ewes the

greatest (approx. 40 μg/100 ml). In proportion to the January level the differences were even more marked (Table 3).

The contradiction in these results is more apparent than real and will be discussed later.

Week of birth

The week in which lambs were born in 1965 was a significant source of variation in the changes of copper level between the summer and the following October and January. In the summer of 1965 the ewes had been bled 6 weeks after parturition. The interval between the summer and October bleeding was therefore greater, the earlier the lambing. Between the first and the last group in the analysis, the average difference in this interval was about 4 weeks. Ewes giving birth to lambs early in the season declined more in copper level than those giving birth to lambs later on. The latest born group showed by far the greatest deviation from average.

The week in which ewes gave birth to lambs in 1966, had a highly significant effect (as a source of variation) on the increase in copper level to June 1966 (all ewes in this case were bled on the same day irrespective of birth date of lamb). However, the changes in copper level associated with each of the 9 weeks of lambing were far from orderly. There was only slight tendency for ewes giving birth late in the 1966 lambing season to have increased more in copper level between January and June (also October and June) than those lambing earlier.

Inbreeding

The differences among the four classes of sheep (0, 25, 37½ and 50 % inbred) in their changes in copper concentration were statistically not significant. It is interesting to note, in a context which will be discussed later, however, that between the summer of 1965 and October the two most highly inbred groups fell by a lesser amount in absolute and proportionate terms than the two less inbred groups. Thereafter, only the most highly inbred group fell less, and subsequently increased less, than the other three groups which were similar to each other.

DISCUSSION

Changes in blood copper levels were associated with the class of sheep. Breed, age and swayback history were the most significant of the factors associated with the amount and rate of decline from the level in the summer of 1965 to that at the end of January 1966. The number of lambs born in the previous year, the number in the current year, age and swayback history were the most significant factors associated with the increase in level from January to June 1966. The week of parturition was a further significant factor but the relative importance of a number of possible components of this effect is not known. These include any effects associated with the date of bleeding (6 weeks after parturition in 1965), the variable interval to subsequent bleedings following that in the summer of 1965 and any separate effects of pregnancy and lactation.

Depending on the extent to which blood copper levels alone describe the availability of copper for maintaining the animal's health and productivity, the effects attributable to the number of lambs born to the ewe (Tables 2, 3) can be interpreted as a response to additional demands on copper as a result of the combined effects of pregnancy and lactation. Butler (1963) reported a fall during pregnancy but a rise after parturition, but McDougall (1947) reported no changes in levels during pregnancy or lactation. In the present experiment ewes barren in 1965 fell less in blood copper level between the summer of 1965 and the following October (and the following January) than did those with lambs. The twenty ewes barren in 1966 included seven which had also been barren in 1965. In January, these seven had a higher blood copper concentration (67 μg/100 ml) than the thirteen barren for the first time (38 μg/100 ml). However, the June levels of the sheep barren in 1966 were higher than those of ewes with lambs. Corresponding, but much smaller differences were apparent between ewes with singles and those with twin lambs.

The association noted between changes in copper levels and age of ewe does not however lend itself readily to an interpretation in terms of demands on copper resources. It seems reasonable to assume that the demands of pregnancy and lactation and residual body growth would bear more heavily on young sheep yet the younger the sheep the greater was the observed increase in copper level over the period including pregnancy and lactation (January–June). Also, no significant interaction was found when the data were tested for an age × number of lambs interaction. Alternative or additional hypotheses thus seem called for to explain the orderly differences associated with changes in age.

Butler & Barlow (1963) reported that copper levels of young females pregnant for the first time fell more during pregnancy than did the levels of older ewes and that after parturition these levels did not rise as far as the older sheep. Whilst this would conform to the idea that the physiological demands on young sheep during this period are greater than those on older ones, Butler & Barlow attributed their finding to the fact that the g

mers had only recently been introduced to the flock and had started with a higher copper level than the older, indigenous ewes.

There appeared to be a tendency for classes relatively high in blood copper to decline less from summer to winter than classes lower in blood copper level. This was clearly apparent in some comparisons—for example, that between ewes with a history of swayback and 'normal' ewes—but it was also seen as a trend among the classes represented by breeds, ages, previous lamb numbers, weeks of lambing, and inbreeding. Moreover, the greater the average fall in level of a class of sheep from summer (1965) to January (1966) the greater the subsequent rise to the following summer (1966). While recognizing that with any three successive measurements, subject only to random and mutually independent errors, the fall is necessarily positively correlated with the rise (merely because the intermediate measurement is common to both), this effect is unlikely to account for the associations found between classes since in previous studies (e.g. Wiener *et al.* 1969) such differences between classes were found to be real and repeatable. The results suggest therefore that sheep with relatively higher copper concentrations in the blood may be less sensitive to changes than sheep with relatively lower concentrations.

The reason why some classes of sheep apparently maintain copper levels in the blood on a more even keel than others is a matter for speculation. One possible mechanism could be related to the amount of copper stored in other tissues, notably in the liver. If the animals in the present experiment conformed to the curvilinear relationship between blood and liver copper concentrations demonstrated by, for example, MacPherson, Brown & Hemingway (1964) and Wiener & Field (1969), a fall in liver copper concentration for animals with a high liver copper status would be expected to be reflected by a smaller decline in blood copper level than would a corresponding fall in liver copper level for animals already lower in liver copper status. Wiener & Field (1969) suggested, however, on the basis of a sample of animals from the present experimental flock, that the level of copper maintained in the blood may be influenced by genetic factors which are not entirely dependent on those affecting levels in the liver. In particular, Blackface × Cheviot and Blackface × Welsh sheep which had, on average, high blood copper levels (like the 'higher' of the parent breeds) had much lower liver levels (like the Blackface). These two crosses might therefore be expected to have an above-average fall in blood copper level over the summer–winter period. However, there is no clear evidence of that in Table 2. More experimental evidence is required and particularly knowledge of liver copper levels of the animals concerned in order to elucidate the mechanisms involved.

The copper injection given to all the ewes in February 1966 and possibly the injection given a year previously is clearly pertinent to the interpretation of the changes in copper levels. Whether seasonal changes would be similar in the absence of this administration of copper is at present under investigation. Clearly also, the factors found to be important as sources of variation in the amount and rate of change in copper level may differ given other sets of conditions. The farm, however, is fairly typical of recently improved and intensively managed upland grazings where there are some indications of copper deficiency.

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GENETIC VARIATION IN COPPER METABOLISM OF SHEEP

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THE purpose of this paper is to review some of the evidence, which has been obtained over the past four years, suggesting that there is genetic variation in the copper metabolism of sheep.

MATERIAL

The evidence is derived from two genetically diverse flocks of sheep on two farms in Peeblesshire, Scotland. The salient feature of management in both flocks is that the different genetic classes are treated alike. Each flock was run as a unit in fields of sown pastures. Details were given by Wiener (1966) and Wiener *et al.* (1969).

Flock 1. The sheep belonged to three breeds: Scottish Blackface, Cheviot and Welsh Mountain and the crosses between them. Crossbred lambs were themselves the offspring of crossbred parents (each parent being the same cross e.g. (Blackface x Cheviot) x (Blackface x Cheviot)). Both purebred and crossbred sheep are represented at different levels of inbreeding (0, 25, 37·5, 50 and 59 per cent.). The ewes were aged from 2 to 5 years old at lambing. The flock has been closed to females since 1955 and to males since 1958. There are approximately 300 breeding ewes in the flock, with younger stock in addition.

Flock 2. About 200 four-year-old Scottish Blackface ewes and a few Blackface x Swaledale ewes were mated to each of two rams from each of five breeds: Border Leicester, Clun Forest, Dorset Horn, Finnish Landrace and Merino. Part of the evidence is derived from the offspring of these matings. Further evidence comes from the next generation obtained by mating females of each of the five crossbred types to each of two rams of each of three further breeds: Oxford Down, Southdown and Soay.

RESULTS AND DISCUSSION

Swayback

In 1964 about 15 per cent. of the lambs born alive in flock 1, and 12 per cent. of those in flock 2, were lost from swayback, mostly of a delayed type. There were, however, considerable differences attributable to breeds (flock 1) and to sires (flock 2). In flock 1, nearly 40 per cent. of Blackface lambs showed ataxia, 11 per cent. of the Cheviots and none of the Welsh. Crossbreds had incidences approximately intermediate between those of the pure breeds contributing to the cross. Level of inbreeding had no apparent effect on the incidence. In flock 2 the offspring groups of particular sires varied in swayback incidence from 0 per cent. to 35 per cent. Details were given by Wiener (1966) and Wiener and Sampford (1969) who also showed that the effects of breed and of sire were statistically significant even after adjusting for effects of weight of ewe and of lamb which vary considerably, as a result of the choice of breeds. Probability estimates for the occurrence of swayback in relation to genetic factors varied from 0 to 80 per cent.

Copper in Blood

Flock 1. Sheep were first bled in January 1965, nine months after the outbreak of swayback. Copper levels in whole blood were found to differ markedly between the breeds. Crossbreds had concentrations of Cu in their blood approximately at the level shown by the pure breed with the higher level contributing to the cross (Wiener and Field, 1966). The adjusted breed values (derived from an analysis involving 'fitting of constants') are shown in Figure 1.

Immediately following this bleeding, the ewes were injected with 50 mg. of Cu (as CuCaEDTA, 'Coprin', Glaxo Laboratories) as a prophylactic measure against swayback. The sheep were bled again four months later and then at intervals for a year. Figure 1 shows that in spite of large changes in average levels of Cu the ranking of the three pure breeds was unaffected and the crossbreds continued to show a marked heterotic effect.

Twenty of the ewes which had produced swayback lambs in 1964 had been retained. Figure 2 shows that their blood Cu levels were indistinguishable from those of their normal contemporaries in the summer but significantly lower in winter (the sheep were from 5 to 12 weeks pregnant in January).

The greater seasonal fluctuation in Cu level of the 'swayback' group is mirrored by differences in the fluctuations of the breeds

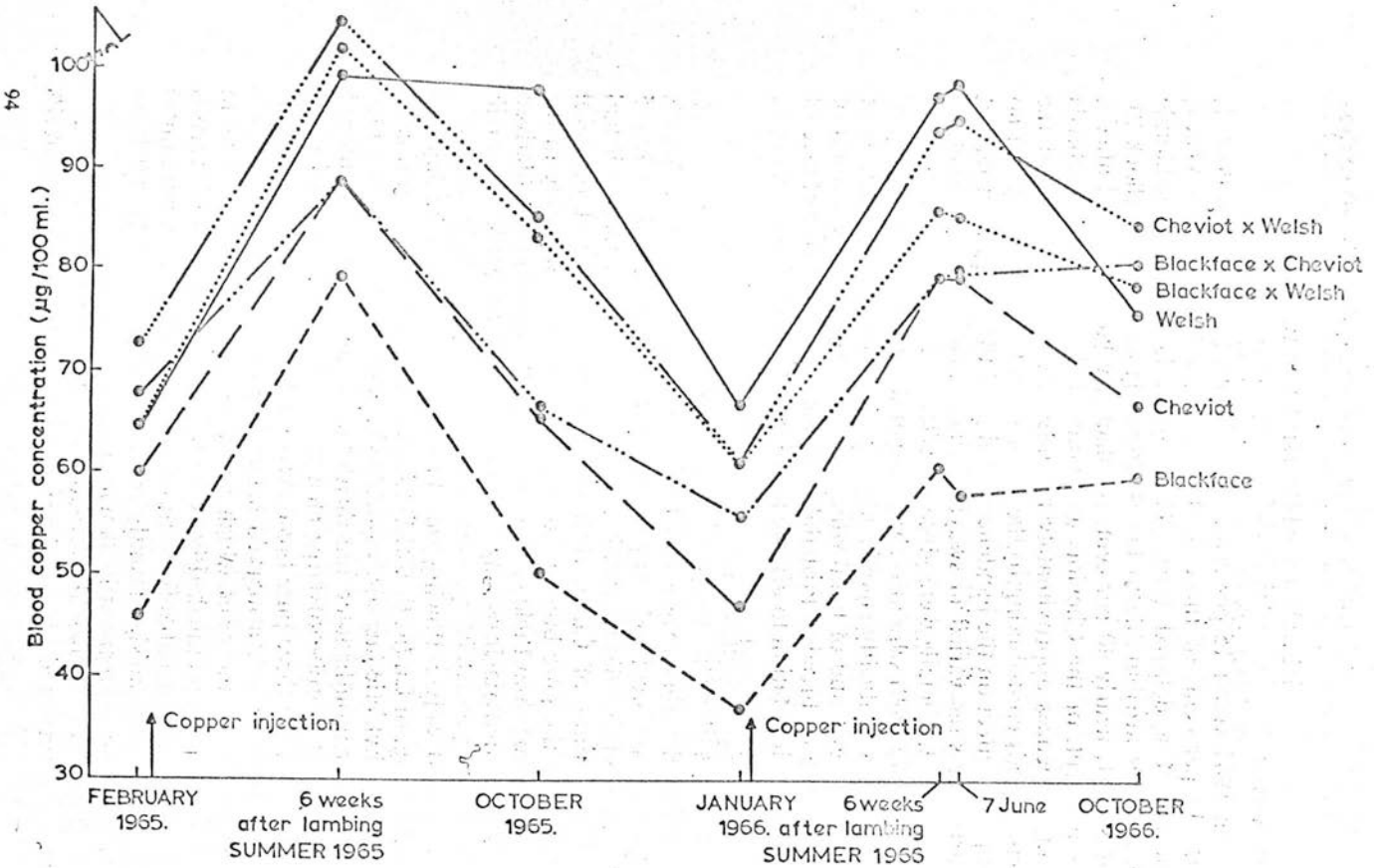

FIG. 1. Concentrations of Cu in the whole blood of six breed classes of sheep on seven occasions when other factors of variation are held constant. The adjusted mean of the flock is included in the breed values. (First and last points on the graph are based on samples of ewes drawn from the flock.) (From Wiener, Field and Wood, 1969, reproduced by courtesy of the editor of the Journal of Agricultural Science, Cambridge.)

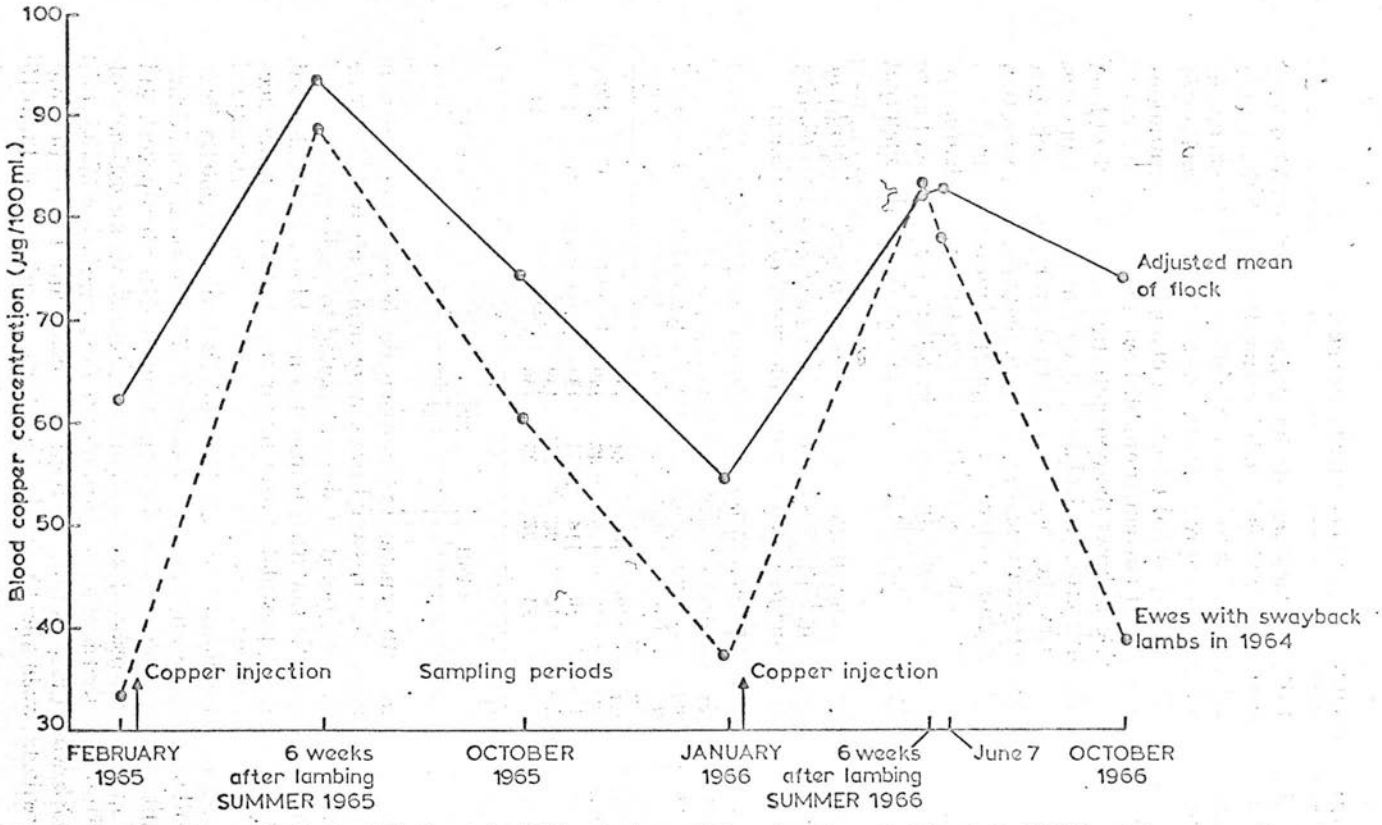

FIG. 2. Concentrations of Cu in the whole blood of adult female sheep which produced swayback lambs in 1964, in relation to the adjusted mean of the flock, at seven subsequent occasions. (From Wiener, Field and Wood, 1969, reproduced by courtesy of the editor of the Journal of Agricultural Science, Cambridge.)

in Figure 1. The Blackfaces declined most and the Welsh least between the summer of 1965 and January 1966. Relative to the starting point of each breed, the breed differences in the change of concentration appear more dramatic. Statistical confirmation of the significance of the breed effects on changes in concentrations has been obtained in current (unpublished) analyses.

Flock 2. Table I shows the concentrations of Cu in the blood plasma of the five crossbred classes of ewe and in that of their lambs. The figures shown are unweighted averages of sub-class means. Preliminary statistical analysis has shown that the variation among breeds of dam and variation among lambs attributable to sire breed is significant ($P < 0{\cdot}01$). The most important feature of the breed variation shown in this table is that two of the columns show variation attributable to breed of sire only—the maternal

Table I. *Copper concentration in the blood plasma (μg/100ml.) of adult ewes and their 15 week-old lambs. (The ewes were the offspring of Scottish Blackface mothers and the breed of sire shown)*

Sire of ewes (maternal grandsire of lambs)	By breed of ewe				By breed of sire		
	Ewes		Lambs		Sire of lambs	Lambs	
	No.	Cu	No.	Cu		No.	Cu
Border Leicester	29	105	44	149	Oxford	87	130
Clun Forest	36	116	47	149			
Dorset Horn	38	114	53	137	Southdown	80	137
Finnish Landrace	42	98	83	139	Soay	88	156
Merino	33	88	28	136			
Significance of breed variation (P)	< 0·01		NS			< 0·01	

contribution, both genetic and non-genetic, being either constant (the mothers of the crossbred ewes were nearly all Blackface) or averaged out (each breed of sire was mated to each crossbreed of ewe). Non-genetic maternal transmission of blood Cu levels need not therefore be postulated as a major cause of breed differences in adult sheep.

The regression of the Cu level in the lambs on that in their mothers, within sire groups, was 0·22 (95 per cent. confidence limits 0·09 to 0·35). Twice this regression (0·44), when parent and offspring are observed at the same age, represents an estimate of heritability, that is the proportion of the total variation in the trait which would respond to selection. However since the relationship here is between the Cu level of adult ewes and that of their 15

week old lambs the heritability estimate is valid only if the trait in the lamb and the adult can be regarded as being the same. Maternal transmission of Cu from the mother to her lamb could affect the magnitude of the regression.

Copper in Liver

In October 1966, a sample of 68 sheep representing all the breeds from flock 1 were slaughtered. The breed variation in liver and blood Cu levels (see Wiener and Field, 1969) is shown in Table II. The Blackfaces and their crosses were low in liver Cu whilst Cheviot, Welsh and Cheviot x Welsh values were higher and not very different from each other. The marked effect of the Blackface genotype on the liver Cu level of crosses with the Blackface contrasts with the positive heterosis shown by the blood Cu level of crosses.

Lambs in flock 1 which had died between birth and weaning (at 15 weeks old) in 1967 and 1968 had their liver Cu concentration

Table II. *Copper concentrations of liver (p.p.m. D.M.) and of whole blood (μg/100 ml.) of three breeds of female sheep and their crosses. (Fitted values obtained by least squares)*

		Cu in liver		Cu in blood	
	No. of animals	Fitted value	SE	Fitted value	SE
Blackface	12	14·3	13·8	59·8	7·6
Cheviot	7	44·7	17·0	66·8	9·4
Welsh	13	49·7	13·1	75·7	7·2
Blackface x Cheviot	12	26·2	14·3	80·8	7·9
Blackface x Welsh	12	23·2	13·9	78·6	7·7
Cheviot x Welsh	12	54·9	13·6	84·4	7·5

(From Wiener and Field, 1969, reproduced by courtesy of the editor of *J. comp. Path. Ther.*)

determined as part of a detailed post-mortem examination. Deaths were attributed to a multiplicity of causes and were not associated with an outbreak of any specific disease (MacLeod and Barlow, unpublished). Results, without regard to cause of death (Table III) show variation in liver Cu concentration attributable to breed ($P < 0{\cdot}002$) and to age at death ($P < 0{\cdot}001$). These, along with the week of birth of the lamb, were the most important of the readily identifiable sources of variation. The ranking of the three pure

breeds among the lambs agrees with that among the sample of adults shown in Table II. Crossbred lambs, however, had Cu levels which, on average, were not significantly different from the levels intermediate between those of the pure breeds represented. The depressing effect of the Blackface genotype on liver Cu noted for adults (Table II) was not observed.

The age trends are interesting in showing a decline with increasing age at death. The values for lambs dying within two days of birth (Table III) are also clearly higher than the values for adults shown in Table II. Unless lambs which died and which are from ewes injected with Cu during mid-pregnancy are atypical of lambs in general in respect of liver Cu, this finding appears to conflict with evidence quoted by Underwood (1962) that, unlike the young of most species, newborn sheep do not have markedly higher levels of liver Cu than adults. Riley *et al.* (1961) have, however, reported that the concentration of Cu in the liver of normal live lambs

Table III. *Copper concentration (p.p.m. of D.M.) in liver and brain of* 166 *lambs which died between birth and weaning in* 1967 *and* 1968. (*Adjusted breed values* and adjustment factors for age at death*).

	No.†	Liver Cu	Brain Cu
Breed:			
Blackface	18	128	9·1
Cheviot	24	140	9·9
Welsh	17	241	12·9
Blackface x Cheviot	50	161	10·7
Blackface x Welsh	27	161	10·8
Cheviot x Welsh	30	168	10·1
Range of SE of differences‡		±21·4–29·6	±0·9–1·2
Age at death:			
Still born	41	0	0
New born	27	14·6	−0·21
1 – 2 days	52	15·6	0·40
3 – 7 days	11	−57·6	−0·16
1 – 6 weeks	16	−46·8	0·89
6 – 15 weeks	19	−135·3	0·10
Range of SE of differences‡		±18·3–32·3	±0·7–1·3

* The breed values are for stillborn, single, 25 per cent. inbred female lambs in 1967 born to 1st parity, F_2 dams in the 1st week of lambing.

† Number of animals available for estimate.

‡ The higher SE's apply to the values with lower numbers of observations and vice versa.

within 24 hours of birth was significantly higher than that of their dams and that by 3 months old the levels in lambs had fallen. In the present study not all breeds were represented at each age of death among the lambs which died; although the linear model used for fitting constants provides an estimate for every class. It should not, however, be inferred from Table III that Blackface lambs dying between 6 and 15 weeks old had no Cu in their livers. The high standard errors allow for ample possibility of positive values. The inference to be drawn is that Blackface lambs had lower liver Cu levels than lambs of the other breeds and that lambs of the oldest age class had a lower concentration than those dying within 2 days.

Copper in Brain

Copper concentration in the brain was also determined for the lambs referred to above. Table III shows significant breed effects ($P < 0{\cdot}05$) and an absence of age effects. The ranking of the three pure breeds was as for blood and liver Cu; crossbreds were intermediate in level between the levels of the pure breeds involved.

Deaths Following Copper Injection

In February 1969, as in the four previous years, ewes were given a subcutaneous injection of 50 mg Cu (as CuCaEDTA) but only 280 out of the total of 360 ewes were treated. Ten of the 280 injected ewes died within three days of injection and an eleventh ewe died three weeks later. The clinical history, taken in conjunction with the post mortem findings (which were similar in all cases except the last sheep to die), strongly suggest that the deaths resulted from the Cu injections, the lesions being compatible with those described for 'acute' Cu poisoning (Watt and MacLeod, unpublished). The live weight of the sheep which died varied considerably and deaths were not confined to small sheep. Liver Cu concentrations ranged from 107 to 357 p.p.m. D.M. (average 196). In the present context the interesting feature of the results is that the deaths were associated with the breeding of the sheep. The 11 which died were Welsh Mountain (4) or a cross with Welsh (7). There were no Blackface, Cheviot or Blackface x Cheviot among the dead whereas five would have been expected in proportion to the numbers injected. The difference between Welsh and non-Welsh representation is significant on a χ^2 test ($P < 0{\cdot}001$).

CONCLUSIONS

The evidence from the two flocks shows clearly that genetic factors influence the concentrations of Cu in blood, liver and brain of sheep. The Cu associated syndrome of swayback, and possibly the susceptibility to Cu poisoning, are also affected by genotype. Crossbred sheep have clearly more Cu in their blood than the midparental level but, on more limited evidence, crossbreds are possibly no more resistant to swayback and may not store more Cu in their livers than the average of the corresponding pure breeds. The results provide a hint therefore of some independence of the genetic mechanisms affecting Cu in blood, in liver and in the incidence of swayback. This hypothesis will require experimental verification.

The evidence for genetic variation in Cu concentrations of blood and tissues and in swayback incidence makes it seem possible that some of the susceptibility of particular farms to outbreaks of swayback should be attributed to the type of sheep kept. In many cases, with particular sheep tied to (and 'acclimatized to') particular farms, the relative contribution of each to the occurrence of swayback must be difficult, or impossible, to determine. However, a reappraisal of past reports of swayback outbreaks in the light of the genetic evidence might be worthwhile. The evidence of genetic variation in Cu concentrations also suggests that there may be more than one 'normal' range for all sheep. The levels below and above which disorders arise may not be the same for all sheep. Some evidence of this was given by Wiener *et al.* (1969).

Future work is aimed at elucidating the physiological mechanisms which give rise to the genetic differences. Evidence of genetic variation in mineral concentration is not, however, confined to Cu (for evidence in other minerals see Field *et al.*, 1969). The opportunity would seem to exist therefore, for catering more precisely for the mineral requirements of genetically different groups of sheep under those conditions where nutrition is readily controllable as, for example, in housed sheep. For large areas of the world, where sheep are kept under extensive conditions, there is at least the hope that sheep can be genetically fitted to the mineral deficiencies, or occasionally the excesses, of those environments.

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The concentration of minerals in the blood of genetically diverse groups of sheep

V. Concentrations of copper, calcium, phosphorus, magnesium, potassium, and sodium in the blood of lambs and ewes

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SUMMARY

Concentrations of Cu, Ca, P, Mg, K and Na were examined in the blood plasma (whole blood for P) of 149 adult ewes and their 244, 15-week-old lambs in a grassland flock of sheep. The ewes were 3 or 4 years old and of five crossbred types produced by mating Scottish Blackface females to Border Leicester, Clun Forest, Dorset Horn, Finnish Landrace and Tasmanian Merino rams. The lambs in turn were the offspring of these crossbred ewes, and two rams of each of the Oxford Down, Southdown, Soay breeds and one Cheviot ram.

Breed of sire (but not sire within breed) was a significant source of variation in the concentration of all the minerals, except Na, in the blood of both ewes and lambs. Other factors considered were age of ewe and sex, birth type, type of rearing, and date of birth of lamb. None of these appeared to be significant sources of variation except that twins and triplets, if reared as such, had higher concentrations of Ca in their blood than lambs born and reared as singles; however the ewes with singles were on different pasture from those rearing 2–3 lambs. For the mineral levels in the blood of the lambs there was no significant interaction of breed of ram with cross-breed of ewe. The lambs had substantially higher concentrations of Cu and P in their blood than their mothers and also significantly higher concentrations of Ca, Mg and possibly K. This may not be attributable to age alone because the lambs and their mothers also differed in genotype.

Heritability estimates based on parent–offspring regression were $0{\cdot}4 \pm 0{\cdot}14$ for Cu and less than 0·2 for the other minerals.

INTRODUCTION

Genetic differences in the concentration of minerals in the blood of sheep have been reported in previous papers (Wiener, Field & Wood, 1969; Field, Wiener & Wood, 1969). Genetic variation has also been shown in the incidence of the disorder 'swayback' which is associated with copper deficiency (Wiener, 1966; Wiener & Sampford, 1969) and more recently there has been a suggestion that the response to an excess of copper in the form of an injection may also be subject to breed variation (Wiener & MacLeod, 1970).

The present paper, the last of the present series, extends these studies by examining the concentrations of copper, calcium, phosphorus, magnesium, potassium and sodium in the blood of sheep of a number of different crosses. Genetic relationships between parents and offspring are also examined.

MATERIALS AND METHODS

The sheep, both ewes and lambs, were bled on 1 August 1967. The ewes involved were the offspring of Border Leicester, Clun Forest, Dorset Horn, Finnish Landrace and Tasmanian Merino rams out of old Blackface and a very few Blackface/Swaledale mothers. The ewes were born in 1963 and in 1964. In each year, it was the aim to mate two rams of each breed to the old Blackface females; however, only one Border Leicester ram was available

in 1963 and one of the Dorset Horn rams was used in each of the two years. The surviving crossbred females produced by these matings were, in 1966, mated to two rams of each of three breeds, the Oxford Down, the Soay and the Southdown, and a single Cheviot ram used as a chaser. The lambs bled in 1967 were thus; $\frac{1}{4}$ Blackface, $\frac{1}{4}$ of the maternal sire's breed and $\frac{1}{2}$ of their own father's breed. Each type of ewe was allocated randomly and in about equal number to each type of ram. The lambs were born from 8 April onward until the end of May but more than 80% had been born before the end of April. The average age of the lambs at the time of bleeding was approximately 15 weeks, the time when they were also weaned.

The management ensured that the different breeds were treated alike, but some disproportionate treatment may have arisen from the fact that ewes rearing single lambs were kept on improved natural hill grazing, whilst ewes with twins or larger numbers of lambs were kept on sown grass in paddocks. The various cross-breeds of ewe had different lambing rates (see Donald, Read & Russell, 1968); thus, for example, a different proportion of the Finnish Landrace crosses would be kept in paddocks than of the Tasmanian Merino crosses.

In February of each year since 1965, the ewes in this flock were given a subcutaneous injection of a commercial preparation of copper calcium EDTA supplying 50 mg of copper as a prophylactic measure to prevent swayback.

Further details of the management of this flock at the farm of Broughton Knowe in Peebles-shire were given by Donald, Read & Russell (1968) and by Wiener (1966).

Statistical analysis

This took the form of fitting a linear model with parameters representing the effects of breed of ewe (i.e. variation attributable to the breed of the sire of the ewes), ram breed mated to these, the sire within each breed involved (taken as a deviation from the mean of the sires of each breed), age of ewe, the number of lambs born per ewe and the type of rearing, the sex of lamb and the stage of the lambing period when the lamb was born (the period was divided into three 10-day stages and a fourth including all the late-born lambs). The interaction of the breed of ewe with breed of ram to which she was mated was calculated separately. Offspring–dam regressions were calculated from residual variances and co-variances after constants had been fitted. Intra-sire half-sib correlations were calculated using sire and residual-variance components after adjustment for the other sources of variation. The analyses were carried out for the six minerals on both ewe and lamb, and the relationship of mineral concentrations to weights of lamb and of dam were also examined.

Estimation of mineral concentrations

Blood samples were obtained from the jugular vein using evacuated heparinized tubes, and the concentrations, except for copper, determined as described previously (Field, Wiener & Wood, 1969). Copper was determined by atomic absorption. The time taken and the absorption obtained were measured when 1 ml plasma was aspirated and the time used to correct for differences in rates of nebulization between individual plasma samples and standards.

RESULTS

The average values of the mineral concentrations in the blood of the animals in this flock (prior to any statistical adjustment for disproportionate representation of the various classes of sheep) are shown in Table 1, both for the 15-week-old lambs and their 3- or 4-year-old mothers.

The factors considered in the statistical model as sources of variation and their significance are shown in Table 2. Few of the factors studied other than breed of sire were significant sources of variation for the concentration of these minerals in the blood of the lambs or in the blood of their mothers. There were, however, some exceptions and these will be referred to in the more detailed consideration of each set of parameters. There were no significant interactions of breed of ram (Oxford Down, etc.) with cross-breed of ewe (Border Leicester cross, etc).

Breed

Estimates of the effects of breed of sire on the mineral concentrations, when other factors in the analysis were held constant, are shown in Table 3 as deviations from the adjusted mean.

Although breed of sire was a significant, or nearly significant, source of variation for all minerals both in lambs and ewes, except for Na, the breed

Table 1. *Overall flock averages for mineral concentrations* ($\mu g/100\,ml$ *for Cu,* $mg/100\,ml$ *for others*) *in the plasma of sheep's blood* (*whole blood for phosphorus*)

	244 lambs		149 ewes	
	Overall mean	S.E.	Overall mean	S.E.
Cu	139·2	2·5	105·1	3·1
Ca	11·10	0·05	10·15	0·1
P	8·17	0·09	5·55	0·2
Mg	2·30	0·01	2·16	0·0
K	30·71	0·31	29·19	0·5
Na	374·9	1·6	372·9	2·1

Table 2. *The significance as sources of variation of a number of factors in mineral concentrations in the blood of* 244 *lambs (approximately* 15 *weeks old) and of the* 149 *mothers of these lambs*

Source of variation		Probability* (%) that variation due to a particular source was due to chance					
Lamb data	D.F.	Cu	Ca	P	Mg	K	Na
Breed of sire of lamb	3	0·01	2	0·01	0·02	0·01	NS
Deviation of individual sires (within breed) from mean of sires	3	20	NS	10	NS	20	NS
Breed of maternal grandsire†	5	20	NS	NS	20	NS	2
Sex of lamb	1	NS	NS	NS	NS	NS	NS
Age of mother	1	NS	10	NS	NS	2	NS
Birth type and rearing	5	NS	2	NS	NS	1	NS
Stage in lambing period when born	3	20	NS	2	NS	NS	20
Interaction: breed of sire × breed of dam‡	12	20	NS	NS	NS	NS	NS
Ewe data							
Breed of sire of ewe†	4	1	10	5	2	20	NS
Deviation of individual sires (within breed) from mean of sires	13	NS	NS	20	NS	NS	20
Breed of mate	3	5	NS	NS	NS	NS	NS
Age of ewe	1	NS	NS	NS	NS	NS	NS
No. of lambs born and reared	5	5	NS	NS	NS	NS	NS
Stage in lambing period when lambs born	3	NS	NS	NS	NS	NS	NS

* Probability % equal to or less than the value shown. NS represents $P > 20\%$.
† The dams of the ewes (maternal grand-dams of the lambs) were nearly all Scottish Blackface.
‡ Interaction not fitted simultaneously as part of model with the other parameters but calculated separately.

differences were particularly marked in the case of Cu. Soay-cross lambs had values on average 26 μg per 100 ml of blood above the average for the flock whilst Cheviot-cross lambs had values 35 units below that average. In the case of the blood of the ewes, the concentrations of Cu ranged from 15·5 units above the mean for Clun Forest × Blackface ewes to 18·5 units below the mean for Finnish Landrace × Blackface ewes. The variation among the breed means in relation to the overall flock mean is shown in Table 3 as the coefficient of variation. It allows direct comparison among the six minerals of the relative importance of variation attributable to breed of sire.

Sire variation within breeds

For the lambs, differences in the mineral concentrations between the offspring of each of the two sires used of each of the three breeds (Oxford Down, Southdown and Soay) came closest to statistical significance in the case of Cu, P and K. These were the minerals where variation among breeds of sire was greatest.

Judged on the mineral concentrations in the blood of the ewes, differences among the rams of each of the five breeds (which were the fathers of the ewes) were not even approaching statistical significance.

Age

Age entered into comparisons of ewes with lambs, into differences between lambs from 3-year-old and 4-year-old ewes, and into differences between the two age classes of ewe.

It can be seen from Tables 1 and 3 that Cu and P levels of lambs were substantially higher than those of ewes. Ca and Mg levels (and K levels when judged on the overall mean alone) were also slightly (but probably significantly) higher for lambs than for ewes. These differences, however, cannot be entirely attributed to age since the comparison is confounded with the difference in the genotypes of the ewes and their lambs.

Blood of lambs from the 4-year-old mothers had $1{\cdot}23 \pm 0{\cdot}5$ mg K/100 ml and $0{\cdot}2 \pm 0{\cdot}1$ mg Ca/100 ml more than blood of lambs born to the 3-year-old ewes. Other differences attributable to age of mother were not significant.

The effect of age (3 *v.* 4 years old) on the concentrations of minerals in the blood of the ewes could not be well estimated since only one sire was common to both age groups. None of the differences was significant.

Table 3. *The effects of breed of sire on the mineral concentrations* in the blood of 15-week-old lambs and of their mothers when other factors in the analysis were held constant*

		Cu		Ca		P		Mg		K		Na	
Lambs	No.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Average adjusted† value	—	129·0	10·1	11·56	0·22	7·63	0·35	2·30	0·06	30·9	1·1	374·8	6·5
Deviation of (sire) breed cross from overall average:													
Oxford Down	76	5·2	7·3	−0·18	0·16	0·28	0·25	0·01	0·04	−0·9	0·8	6·4	4·7
Southdown	73	3·6	6·8	−0·26	0·15	−0·05	0·23	−0·11	0·04	−1·7	0·7	5·5	4·4
Soay	80	26·3	6·6	0·15	0·14	0·86	0·23	0·03	0·04	3·9	0·7	5·8	4·2
Cheviot	15	−35·1	17·6	0·29	0·38	−1·09	0·61	0·06	0·10	−1·3	1·8	−17·7	11·3
Coefficient of variation‡ of breed means (%)	—	79		13		46		23		68		6	
Ewes													
Average adjusted† value	—	77·2	14·8	10·31	0·64	4·91	0·60	2·10	0·14	30·8	2·0	392·9	12·7
Deviation of (sire) breed cross from overall average:													
Border Leicester	28	−0·7	6·6	−0·07	0·28	−0·69	0·27	−0·13	0·06	−1·5	0·9	−2·7	5·7
Clun Forest	30	15·5	6·9	−0·49	0·30	0·23	0·28	0·04	0·06	−0·5	0·9	0·1	5·9
Dorset Horn	30	11·7	6·4	0·51	0·28	0·45	0·26	0·05	0·06	−0·1	0·9	−8·7	5·5
Finnish Landrace	38	−18·5	7·2	−0·48	0·31	−0·42	0·29	0·18	0·07	−0·2	1·0	−1·3	6·1
Merino	23	−8·1	7·8	0·53	0·33	0·43	0·31	−0·14	0·07	2·3	1·0	12·7	6·7
Coefficient of variation‡ of breed means (%)	—	83		22		45		28		19		9	

* For Cu: μg/100 ml, for the other minerals: mg/100 ml.

† The basic class of lamb in terms of which the results are given refers to single-born, female lambs reared as singles on their own mothers, born in the first 10 days of the lambing period to 4-year-old ewes represented by the average of their breeds and the sire breed value represented by the average of the rams used. The basic ewe class refers to 4-year-olds giving birth to and rearing singles (born in the first 10 days of lambing) mated to the average ram of the 'average' of the breeds, and with its own sire's breed value represented by the average of the rams used. The overall average for both lambs and ewes is represented by the mean of their respective sire breeds.

‡ Coefficient of variation of breed means = S.D. of breed means/adjusted mean.

Birth type and rearing of lambs

Any comparison between ewes rearing singles and those rearing more lambs is confounded with a difference in management.

Twins and triplets, especially when reared as twins or triplets, had a lower concentration of Ca in their blood than did single-born lambs reared as singles; mothers of lambs in the various birth-type and rearing categories did not, however, differ significantly in the Ca concentration of their own blood, although there seemed to be a slight tendency for ewes which had given birth to triplets and reared either two or three of their lambs to have slightly the higher concentration. For potassium, differences among birth type and rearing classes were unsystematic, but sufficiently large to be a significant source of variation in the blood of lambs.

Stage in the lambing period when lambs born

When the lambing period was divided into four stages, there was seen to be a clear increase in the concentration of P in the blood of the lambs the later in the year they were born (the younger at bleeding). For Cu and Na the last-born group of lambs differed from the others in having the highest concentrations.

Correlations

Table 4 shows the residual correlations among mineral concentrations when effects of the other factors were held constant. For minerals in the blood of ewes, correlations were in general very small (of the order of 0·2 or less), except some of those involving Ca which were higher, the highest (0·47) being that between Ca and P. The corresponding correlations for mineral concentrations in the blood of the lambs were also small in magnitude. Although small, many of the correlations were statistically significant. The correlations calculated from ewe and lamb data were not in all cases in good agreement. The most marked differences between the two sets of data were in the correlation of Mg with P, which was negative for ewes and of similar magnitude but positive for lambs this difference being statistically highly significant ($P < 0{\cdot}001$). Other correlations where the estimates from ewes and lambs differed significantly ($P < 0{\cdot}05$) were found in respect of Ca and Mg, Ca and Na, and Ca and P.

The partial correlations were of similar magnitude to the corresponding simple correlations shown in Table 3. This suggests that the correlation between any two minerals did not arise from a common relationship with any of the other five minerals.

Correlations attributable to 'breed' of lamb (i.e. 20 classes comprising breed of sire × breed of dam) were statistically significant for 6 of the 15 correlations among the minerals of lamb's blood. The six were: Cu.Ca ($r = 0{\cdot}6$), Cu.K (0·6), Cu.P (0·7), Ca.K (0·6), Ca.P (0·6) and P.K (0·7). There were no significant correlations attributable to the effects of sire of ewe (i.e. 18 sires of 5 breeds) among the mineral concentrations in the blood of the ewes.

None of the mineral concentrations of either the lambs or the ewes was significantly correlated with the body weight of the animal within its respective breed type.

Relations of parent to offspring

For the concentration of each of the minerals the regression of lamb on mother was calculated (as described earlier). The coefficients are shown in Table 5. The regression coefficient for Cu was the highest and statistically significant ($P < 0{\cdot}02$). For the other minerals the regressions were much smaller but approaching significance particularly for Mg and Ca. For Na concentration the regression of offspring on mother was negative and the standard error too small to allow this regression to be immediately dismissed.

Doubling the offspring–parent regression is a standard method of estimating heritability (Falconer 1961). The appropriate estimates are given in Table 5 along with heritability estimates based on four times the intra-sire half-sib correlation. Certain assumptions necessary for the interpreta-

Table 4. *Residual correlations among mineral concentrations in blood plasma (whole blood for P) when the effects of a variety of factors have been removed as sources of variation (see text)*

(Correlations for lambs (242 D.F.) above and for adult ewes (147 D.F.) below the diagonal.)

	Cu	Ca	P	Mg	K	Na
Cu	—	−0·02	−0·02	−0·20**	0·01	−0·00
Ca	−0·19*	—	0·23***	0·14*	0·25***	0·20**
P	−0·08	0·47***	—	0·28***	0·26***	0·03
Mg	−0·09	−0·17	−0·21*	—	0·36***	−0·07
K	−0·07	0·35***	0·23**	0·22*	—	0·12
Na	−0·02	0·44***	0·23**	−0·04	0·20*	—

*** $P < 0{\cdot}1\%$. ** $P < 1\%$. * $P < 5\%$.

Table 5. *Regression coefficients of offspring on dam and heritability estimates for mineral concentrations in blood*

	Regression†		Heritability estimates based on: 2 × offspring dam regression‡		4 × intra-sire half-sib correlation: Ewes (11 D.F.)		Lambs (3 D.F.)	
	Coefficient	S.E.	Coefficient	S.E.	Coefficient	S.E.	Coefficient	S.E.
Cu	0·20	0·07	0·41	0·14	0·07	0·35	0·05	0·16
Ca	0·07	0·04	0·13	0·08	0·24	0·41	0·01	0·12
P	0·07	0·06	0·14	0·13	0·42	0·47	0·27	0·36
Mg	0·09	0·04	0·17	0·09	−0·20	0·33	−0·06	0·11
K	0·09	0·06	0·18	0·12	0·19	0·36	0·03	0·13
Na	−0·09	0·06	−0·19	0·11	0·14	0·35	−0·02	0·11

† Regression of offspring on dam within sire group (after adjustment for environmental variables).
‡ For particular assumptions see text.

tion of these estimates will be discussed later. As expected from the small number of sires involved, the standard errors of the half-sib estimates are high and the corresponding heritability estimates unreliable. They are presented only as a first approximation in the absence of any other published estimates.

DISCUSSION

The average values for the concentrations of the various minerals which were shown in Table 1 indicate that for the flock investigated the values were within the physiologically normal range.

Genetic considerations

Breed of sire contributed significantly to the variation in the plasma concentration of Cu, Ca and Mg and the whole-blood concentration of P of 15-week-old cross-bred lambs and of their cross-bred mothers, and in the plasma concentration of K for lambs alone. This supports evidence of significant breed differences in the concentrations of these minerals in another grassland flock comprising the Scottish Blackface, Cheviot and Welsh Mountain breeds and their crosses (Wiener, Field & Wood, 1969; Field, Wiener & Wood, 1969). For housed sheep fed on dry-lot until weaning, Long *et al.* (1965) found no consistent significant difference among the Hampshire, Suffolk and Shropshire breeds in the concentrations of serum Ca, P, Mg, Na and K. Becker & Smith (1950) with Corriedale, Dorset and Hampshire breeds (also housed for part of the year) also reported an absence of significant breed differences for plasma Ca and P, but only 18 sheep were involved. Eagleton, Hall & Russell (1970) have reported that K concentrations in plasma were influenced by *Ka* genotype and breed.

In the present investigation, unlike in the earlier ones, the maternal breed contribution, both gene and non-genetic, was either 'constant' (t mothers of the cross-bred ewes were nearly Scottish Blackfaces), or 'averaged-out' (each br of sire of the lambs was mated to each of the cross-bred types of ewe). The differences attri table to breed of sire, therefore, were indepen of differences due to breed of dam.

If the values for the mineral concentrations of cross-breds were half-way between the values their respective parental breeds, the simplest of genetic assumptions, the deviations from aver of the pure breeds represented by the rams wo be expected to be twice as large as those shown Table 3 for cross-breds. For example, Cu co centrations of the Oxford Down rams would expected to differ from the Soay rams by μg/100 ml instead of half that difference (between Oxford crosses and Soay crosses. H ever, in the present experiment pure breeds not available for comparison with their cro Deviations from mid-parental values (impl some non-additive genetic variation) would therefore be detected unless they also result interactions between breed of sire and cross-b of dam. Statistical analysis of the lamb data no significant evidence of this; that is to within the accepted limits of probability, ferences between offspring of Oxford D Southdown, Soay and Cheviot rams were same irrespective of which the cross-bred typ ewe was the mother. It is worth noting, how that the estimate of interaction came close statistical significance ($P < 0{\cdot}20$) for Cu element for which deviations from mid-par concentrations were most marked in earlier s (Wiener, Field & Wood, 1969). Evidence of s but statistically significant deviations from parental values had also been reported for Ca

positive direction) and P (in a negative direction) (Field, Wiener & Wood, 1969).

Estimates of heritability were made (i.e. estimates of additive genetic variation in relation to total variation) by comparing variability arising within sire progeny groups with the variability occurring among such groups with breeds. As expected from the inadequate numbers for this purpose, however, the estimates based on half-sib correlations are of little practical use because of the large errors attached to them. None the less they have been recorded (Table 5) as (apparently) the first approximations published for these parameters and because they can be expected to contribute useful information in conjunction with any future estimates based on different populations.

The relationship of the concentration of each mineral in the blood of the lamb with the equivalent concentration in the dam's blood also yields an estimate of heritability (Falconer, 1961), depending for its validity on the assumptions that the mineral concentration in the lamb is genetically completely correlated ($r_g = 1$) with the concentration for the same animal when adult, and that the heritability in the lamb and in the adult is the same. If these assumptions were not met, the estimates quoted in Table 5 could be too low. For example, variances of Ca and Mg concentrations differed significantly for ewes and lambs. Estimating heritability from twice the dam–offspring correlation, as a means of 'averaging' these variances, yielded higher values (0·24 and 0·26 respectively) than those shown in Table 5. On the other hand, environmental effects which might be in common for the ewe and her lamb, and maternal effects associated with the 'environment' the ewe provides for her lamb, tend to inflate heritability estimates based on the offspring–dam relationship (e.g. see Falconer, 1961). With these reservations in mind, the estimates based on this relationship (Table 5) suggest moderately high heritability for Cu and lower (mainly non-significant) values for the other minerals. The negative offspring–dam relationship for Na was not significant. The implication is that Cu concentrations could be fairly readily changed by selection, but practice might show otherwise in view of the constraints on the conclusions to be drawn from heritability estimates.

Some indirect evidence from this and another flock suggests that copper concentrations in young lambs were correlated with levels of the adults. This evidence showed that losses of lambs from swayback which may be regarded as a form of selection against low Cu values led to a correlated response in the Cu levels of the unaffected adult survivors which had higher levels than did ewes in comparable groups in which no swayback losses had occurred (Wiener, 1971).

Relationships with body weight

In the earlier study involving adult ewes of three breeds and their crosses (Wiener, Field & Wood, 1969) the lightest of these in weight, the Welsh Mountain breed, had clearly the highest Cu concentrations in blood among the three pure breeds. It is interesting to notice therefore that lambs fathered by Soay rams, the lightest of the crosses in the present experiment (Donald, Read & Russell, 1970) also had clearly the highest Cu concentrations in their blood. However, any probability that this arose as a function of body size alone is lessened by the absence of a negative correlation between body weight and copper concentration within breeds (in the earlier study quoted there were in fact small but significant positive correlations of weight within breeds and Cu, Ca and Mg concentrations). Moreover, Oxford Down crosses, the heaviest in the present experiment, or, for example, the heavy Blackface × Cheviot crosses in the earlier study, did not have the lowest average concentrations of Cu in their blood.

Age differences

No significant difference was found between the concentrations of minerals in blood from 3- and 4-year-old ewes. Field, Wiener & Wood (1969) reviewed the literature on age effects and, for the experiment quoted earlier, reported that age over the range from $1\frac{1}{2}$ to $5\frac{1}{2}$ years (not the difference between 3 and 4 years old alone) was a significant source of variation for Ca, P, Mg and K concentrations in blood sampled at the same season of the year as the sheep now investigated (though not the same year).

The differences found between ewes and lambs in the concentrations of several of the minerals may not be interpretable as an age effect alone because of the concurrent difference in the genotypes of ewes and lambs. However, particularly for Cu, P and Ca, these 'age' differences were large in relation to the average differences among the breeds. For concentrations of P in blood, Becker & Smith (1950) and Long *et al.* (1965) reported lower levels of P for lambs than for adults, in agreement with the present results. For Mg concentration the adults studied by Long *et al.* exceeded lambs while the opposite was noted here. For Ca, where our data indicate the lower level in adults, Long *et al.* observed little change from about 3 months of age onward although the levels in younger lambs were higher. Becker & Smith (1950) and Hackett, Gaylor & Bustad (1957) found no significant difference for Ca concentration in the blood of Suffolk ewes and their lambs. The fact that the lambs in the present experiment were reared with their mothers at pasture whilst those in other experiments were not, may well affect the results.

The markedly higher level of Cu in the blood of the 15-week-old lambs compared with that of their mothers studied here, if interpreted as an age effect, is not reported elsewhere in the literature on sheep as quoted by Underwood (1962).

Correlations among mineral concentrations

Residual correlation coefficients among the concentrations of the six minerals in the present study were not in very good agreement with the coefficients published by Wiener & Field (1969), six of the fifteen differing significantly. The most marked differences were in the coefficients describing the relationship of Cu with Ca, Ca with P, and Mg with P. For the most part, however, the correlation coefficients were small, suggesting as before that within breeds most of the variation in the concentration of any one mineral was independent of that of any of the other minerals.

The concentrations of several of the minerals in the blood of the lambs (but not in the blood of the ewes) were found to be significantly correlated ($r = 0{\cdot}6$ to $0{\cdot}7$) by virtue of the effects of the breeding which they had in common. Correlations attributable to the effects of breeds were also reported by Wiener & Field (1969). Since the two experiments utilized different sets of breeds, the fact that some of the corresponding correlations differed in sign could be the result of breed variation in the relationship of one mineral with another. It could also be the result of different environmental circumstances in which the two experiments were carried out.

CONCLUSIONS

The studies of mineral concentrations in the blood of sheep, on which this series of papers has been based, have shown that a significant proportion of the variation among individuals can be accounted for by a variety of factors such as breed, age, live weight, number of lambs born and reared, season of year and, in the case of copper, the swayback history of the animal. Not all factors were of equal importance for all minerals and in all circumstances, and in the case of plasma Na little of the total variation could be thus accounted for. Other factors might also be found to be relevant sources of variation for mineral concentrations in different circumstances, as for example stage of pregnancy or milk yield. As a generalization it seems likely that to take cognizance of these sources of variation will allow the significance of nutritional factors to be more easily recognized.

The most novel evidence demonstrated in these papers is that of breed differences in the concentrations of minerals in blood, supported in the case of copper by evidence from liver and brain tissue (Wiener & Field, 1969, 1970). Comparisons of cross-bred with pure-bred sheep also pointed to the importance of non-additive genetic variation, especially for copper in blood. Initial interest in copper arose from the observation of breed differences in the incidence of swayback (Wiener, 1966) and, perhaps for that reason, breed variation was more clearly manifested for copper than for the other six blood constituents also tested.

The practical implications of these findings will depend first on whether genetic differences in blood constituents reflect differences in the animals' requirements for the minerals and secondly on whether even small differences can have crucial effects on mineral metabolism and consequently on productivity.

It is reasonable to assume that the manifestation of genetic variation in the mineral concentrations of sheep blood may vary with the nutrient supply of the minerals concerned. So far, the importance of such genotype–environment interactions remain largely unexplored although recently Wiener, Field & Jolly (1970) have shown the significance, as a special case, the interaction of breed and season of year for the concentrations of copper in blood.

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Genetic variation in mineral metabolism of ruminants

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The occurrence of disorders of mineral metabolism in cattle and sheep, for example hypocalcaemia, hypomagnesaemia or swayback, suggests that some individuals are unable to meet their mineral requirements. The question arises whether such differences among individuals are inherited and can be affected by a breeding policy.

The incidences of most of the metabolic disorders are low and sporadic, even though costly. Generally, under these circumstances little progress can be expected in reducing the incidence of these metabolic disorders in future generations by removing, or allowing nature to remove, only the clinically affected animals from the breeding population. Even such little change as might be expected from natural selection is counteracted by normal husbandry and veterinary practices which preserve deficient individuals by rescuing them from the consequences of disorder or by preventing its manifestation (an example relating to swayback is discussed by Wiener (1971)).

Genetic progress in reducing metabolic disorders is most likely to be made if the underlying biochemical variation is understood, is measurable in apparently healthy animals and is inherited. More urgency is given to finding answers to the appropriate questions if the disorders are expected to increase in frequency as higher

production and intensive husbandry systems impose additional stresses on the animals or, conversely, as ruminants are expected to make increasing use of the extensive, more 'deficient' areas of the world, and of plant and industrial by-products.

Suboptimal performance has also been associated with mineral deficiency or imbalances (Underwood, 1966) and reports in the literature are not uncommon of favourable responses to dietary additions of, for example, cobalt, copper or selenium where no clinical symptoms of deficiency were detected. If genetic variation is demonstrated at the level of clinical disorder, it must also be sought at other points in the scale from disease at one end to optimum performance at the other.

This paper reviews the evidence to date for genetic variation in disorders of mineral metabolism, and in the mineral concentrations in blood, milk, excreta and tissues of sheep and cattle. Some of the results from cattle blood are presented for the first time.

Disorders associated with mineral metabolism

Swayback. Large differences among breeds and among sire progeny groups in the incidence of swayback in lambs were reported by Wiener (1966). The flocks concerned had been self-contained for many years and the different breeds or sire-progeny groups had been born together and treated alike. All sheep were at grass throughout the year. In one flock (subsequently referred to as flock A) the breeds were Scottish Blackface, Cheviot and Welsh Mountain, and the crosses among these. In another flock (B), Blackface ewes had been mated to rams of the Border Leicester, Clun Forest, Dorset Horn, Finnish Landrace and Merino breeds, and the female offspring of these matings had been further crossed with rams of the Oxford Down, Soay and Southdown breeds. A third flock (C) provided a comparison between offspring of Border Leicester and Wiltshire rams. The breed incidences in swayback ranged from 0 to 40% of the lambs born and the differences among sire groups were similar. Since the breeds also differed markedly in body size, it appeared plausible that the variation in swayback incidence might be related primarily to variation in size and hence indirectly to intake of nutrients. Re-analysis of the data after adjustment for the effects of weight of ewe and of lamb, however, confirmed the statistical significance of the genetic variation in swayback incidence (Wiener & Sampford 1969).

Suttle & Field (1969) have reported marked differences in the responses, including the induction of swayback, of groups of sheep derived from different flocks following prolonged experimental depletion of Cu.

Copper poisoning. Prophylactic subcutaneous injections of 50 mg of a copper-calcium complex of EDTA were given to the ewes in flock A in the years following the outbreak of swayback of 1964. Seventeen sheep (1·04% of those injected over a 5-year period) died shortly after the injection and although the risks of death were found to be strongly associated with the dose given per unit live weight of sheep there was also a significant breed difference in mortality (Wiener & Macleod, 1970). It is interesting in this context that in a discussion on Cu toxicity, Marston (1950)

claimed that, under experimental conditions, British breeds of sheep usually succumb to the first haemolytic crisis whereas Merino sheep may survive two or three such crises.

Milk fever. Differences in the breed incidence of this disorder in cattle have been acknowledged for a long time and were shown in the survey by Leech, Davis, Macrae & Withers (1960). Data from various other sources were summarized by Meyer (1968) to give incidences of 13·8% for Jersey, 8·6% for Guernsey, 5·5% for Ayrshire and 4·8% for Holstein. It must be recognized, however, that these different breeds are not normally kept in the same herds and that the breed differences may be confounded with environmental and management differences. Confidence in a genetic effect is, therefore, strengthened by the observation of D. Gibson (unpublished data) that Jerseys had an average incidence of milk fever over five lactations of 18·7% compared with 8·0% for Friesian and 3·5% for Ayrshire in a herd belonging to the Animal Breeding Research Organisation where all three breeds were born and kept together.

J. L. Read (unpublished data) has also recorded a breed difference in losses thought to be due to hypocalcaemia in lactating Swaledale and Blackface ewes run together as a single grassland flock by the Animal Breeding Research Organisation.

Grass tetany. The survey of Leech *et al.* (1960) also showed a breed difference for this source of loss in cattle. The reservations, stated above, about attributing the differences to breed alone apply also to this evidence.

Other disorders. Goitre in lambs has been generally attributed to iodine deficiency or goitrogenic factors but Rac, Hill, Pain & Mulhearn (1968) and Mayo & Mulhearn (1969) have described a similar condition due to the action of a recessive gene. Complex biochemical analysis of this form of congenital goitre revealed not merely the disordered biosynthesis of thyroid hormones (Falconer, 1965) but that sheep heterozygous for the gene, and hence clinically normal, showed, on average, elevated concentrations of iodoproteins in their blood. Unfortunately, the overlap in the ranges of concentrations in normal (homozygous) and in heterozygous sheep prevented the use of this test to detect heterozygotes.

An elegant study by Hurley (1968) of genetic-nutritional interactions involving manganese was carried out on mice. Congenital ataxia occurs in offspring of mice and of many other species given a Mn-deficient diet during pregnancy. A similar condition was observed in mice with the mutant gene *pallid.* The genetically induced condition could, however, be prevented by Mn supplementation of the normal stock diet during pregnancy. Thus, the action of the gene could be masked by nutrition. Hurley was also able to show that the specific pathways of the two conditions differed.

Genetic variation in mineral concentrations

Sheep

Copper. Following the observation of breed differences in the incidence of swayback referred to earlier, Wiener & Field (1966) demonstrated large differences in

the concentrations of Cu in the blood of these breeds of sheep in flock A. Later work showed not only that breed differences persisted in spite of Cu injections and wide seasonal variation in average Cu concentrations of the flock but, that to a limited extent, seasonal variation was modified by genetic factors (Wiener, Field & Wood, 1969; Wiener, Field & Jolly, 1970). Cross-bred sheep were found to have concentrations of Cu in their blood markedly above the mean of the parents in spite of the fact that the cross-breds had had a more nearly intermediate incidence of swayback. It was also observed that groups that had relatively high concentrations of blood Cu fluctuated less in concentration over the year than groups that had relatively low concentrations. Therefore, if it can be deduced that Welsh Mountain sheep, for example (a 'high' group), maintain a better homeostatic control over their Cu metabolism than, for example, Blackface sheep (a 'low' group), the information would point to the possibility of genetically influencing stability by choosing sheep with genetically 'high' concentrations. Payne, Dew, Manston & Vagg (1970) also point to an inverse relationship between mean concentration and variability for concentrations of magnesium in the blood of cows.

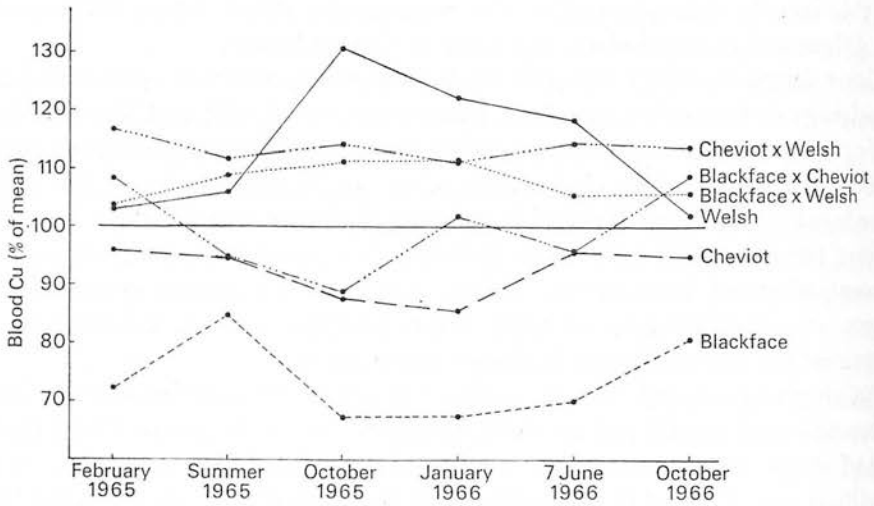

Fig. 1. Concentrations of copper in the blood of ewes of six breed classes expressed as deviations from the mean of the breeds on each of six occasions, in a self-contained grassland flock (data from Wiener, Field & Wood, 1969).

The published data from flock A have been summarized in Fig. 1 to demonstrate the breed differences (as deviations from their mean) and their persistence over six successive bleedings when the actual, average concentrations varied from above 90 μg Cu per 100 ml blood (summer of 1965) to below 60 μg/100 ml (January, 1966).

Fig. 2 shows the behaviour over the same 18-month period of a group of ewes which had produced swayback lambs in a previous year. This demonstrates clearly the relatively greater seasonal fluctuations of the low-Cu class – a feature less readily seen, though statistically demonstrable, for the breed classes.

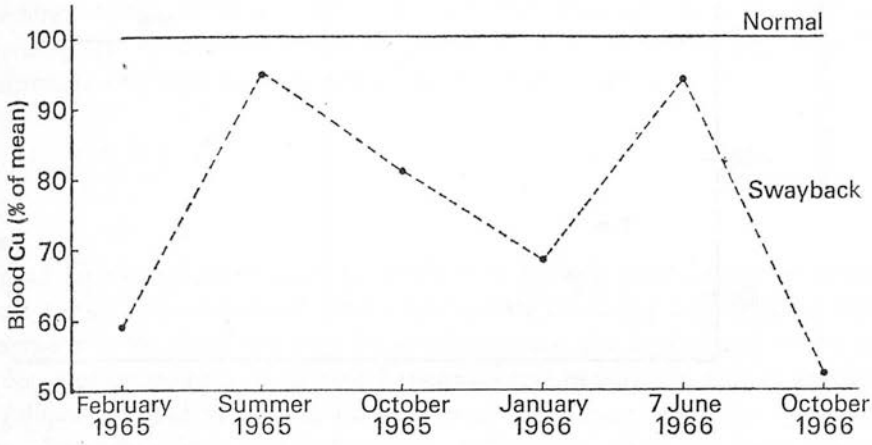

Fig. 2. Concentrations of copper in the blood of a group of twenty ewes, which had produced swayback lambs in 1964, expressed as deviations from the concentrations in the blood of normal contemporaries in the same flock, on each of six occasions (data from Wiener, Field & Wood, 1969).

Evidence of variation in Cu concentration among diverse breed crosses was also obtained from flock B (Wiener & Field, 1971). Lamb-mother regressions calculated for data from this flock also indicated that variation in blood Cu concentration may be genetically variable within breeds but information on differences among sire progeny groups is still totally inadequate to allow prediction of the response of blood Cu to selection. That it can be affected by choice of breed and by cross-breeding seems to be far better established.

Concentrations of Cu in liver (Wiener & Field, 1969*a*) and in brain (Wiener & Field 1970) have also been examined and found to show significant breed variation. Cross-breeding appeared to affect liver values differently from blood values, thus creating genetically four classes which can be, broadly speaking, described as relatively high in both liver and blood Cu concentration, low in both, or relatively high in one and low in the other. This is shown in Fig. 3 by presenting the results of Wiener & Field (1969*a*) as deviations from the means. It may be implied from these results that there is some measure of genetic independence of the control of concentrations in the liver and blood. Also, these results lead one to suggest that the consequences of deficiency or excess of Cu in the feed may differ for each class but that these might, in due course, become predictable because of the genetic basis.

Other minerals. Concentrations of calcium, magnesium, potassium, sodium and chlorine in plasma, and of phosphorus in whole blood were also examined in the two

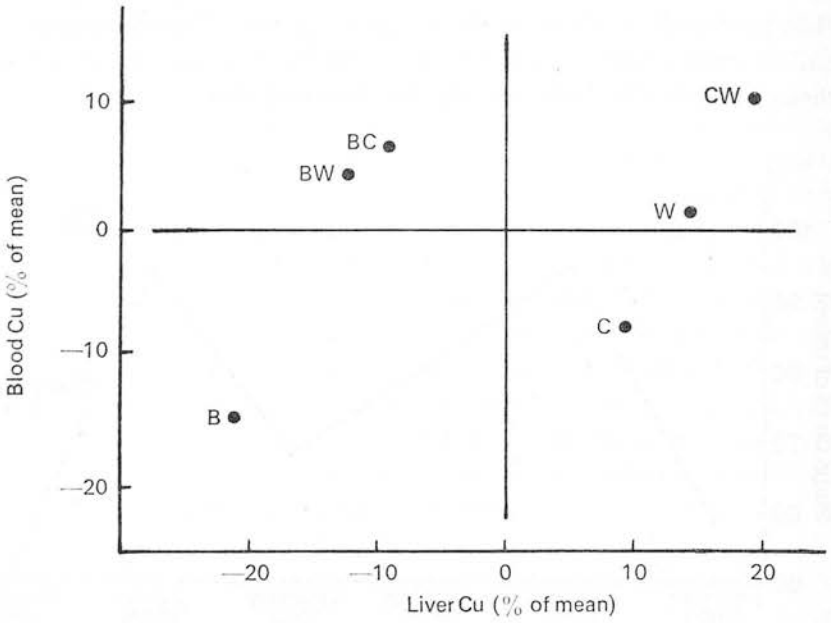

Fig. 3. Breed means for the concentrations of copper in the liver and blood of sixty-eight, 5-year-old ewes expressed as deviations from the mean of the breeds (data from Wiener & Field, 1969*a*). B, Blackface; C, Cheviot; W, Welsh; BC, Blackface × Cheviot; BW, Blackface × Welsh; CW, Cheviot × Welsh.

flocks (A and B). Based on a single bleeding, the results showed significant breed variation for Ca, P, Mg and Cl although the contribution of breed (or cross-breed) to the total variation was less than 10% except for Mg where it was 20% (Field, Wiener & Wood, 1969; Wiener & Field, 1971).

One of the most interesting facts to emerge was that eighteen of the twenty sheep (in flock A) with Mg concentrations below 1 mg/100 ml blood plasma were Cheviots or Cheviot crosses. Ritchie & Hemingway (1963) reported that Cheviot sheep had lower Ca and Mg values than Cheviot × Border Leicester crosses, and Sykes, Field & Slee (1969) observed a difference in Ca concentrations between Southdown and Welsh Mountain sheep. Differences among sires within breed (Wiener & Field, 1971) were not found to be statistically significant but the number of such comparisons and the relatively small number of progeny for each sire made this not surprising, unless genetic effects were overwhelmingly large in relation to variation from other causes.

Several breeds were involved in experiments with housed sheep on dry-lot reported by Long, Ullrey, Miller, Vincent & Zutant (1965). They observed no consistent breed differences in the concentrations of serum Ca, P, Mg, Na and K. Becker & Smith (1950) found no breed difference in plasma Ca and P among a small group of sheep also housed. Eagleton, Hall & Russell (1970) have recently reported an

influence of breed and *Ka* genotype on K concentrations in plasma of grazing sheep.

A population appropriate for a study of genetic correlations among the concentrations of minerals in blood has not yet been sampled but, superficially, the relationships involving breeds (Wiener & Field, 1969*b*, 1971) suggest that genetic changes in the concentration of one mineral may well be accompanied by changes in the concentration of others. The point is further illustrated by the marked genetic relationship of K and Na in whole blood where a gene for high and low K concentration has been demonstrated (Evans & King, 1955).

Cattle

Almost all the evidence capable of yielding genetic information on aspects of mineral metabolism is derived from experiments involving monozygotic twins. If monozygotic twins alone are used in an experiment, the importance of the genetic variation as a proportion of the total (heritability) is nearly always overestimated. The estimate of genetic variation is improved if contemporary pairs of animals of lesser relationship (e.g. dizygotic twins, half-sisters, etc.) are used along with monozygotic twins. Both genetic and environmental components of variation can then be estimated from within pairs, (see King & Donald, 1955). An experiment of this structure has been used for a study of mineral concentrations in blood and some preliminary results are presented.

Blood. Samples were obtained at a single bleeding in November 1969 for five pairs of monozygotic twins, nine pairs of dizygotic twins, twenty pairs of half-sisters and eleven pairs of unrelated animals, all female and with pair members at approximately the same stage of pregnancy and lactation. Pair members of the two non-twin classes were of the same breed, born within a few days of each other and treated alike — for all essential purposes as twins. The animals were part of a continuing uniformity trial first described by Donald (1953). At the time of bleeding all the animals were housed and individually fed.

The genetic analysis on within-pair variation was based on the simplest assumption that all variation could be attributed to a single environmental and a single genetic component, the proportion of the genetic variation depending on the relationship of the pair members. Variation between pairs was not considered. A least-squares solution ensured that the environmental component was not deduced from monozygotic twins alone. The simple assumptions fitted the data well and the results are shown in Table 1 with the genetic variation expressed as a percentage of the total. For K concentration the results were absurd (partial haemolysis in a few samples came to be suspected afterwards) and have been interpreted as indicating zero genetic variation. The estimate of genetic variation for P concentration is little greater than its standard error, but for the other minerals the results suggest a moderately high heritability.

Table 1. *Estimates of genetic variation expressed as a percentage of total variation for the concentrations of various minerals and of glucose in the blood plasma* of cattle from a single breeding†*

	Cu	Ca	P	Mg	K‡	Na	Glucose
Percentage	63	82	46	58	0	81	64
Approximate standard error	27	13	39	31	—	14	26

*Whole blood for P.

†Based on five pairs of monozygotic twins, nine pairs of dizygotic twins, twenty pairs of contemporary half-sisters and eleven pairs of contemporary unrelated females.

‡Estimates were negative with high SE — interpreted as implying zero genetic variation.

Indications from other sources for genetic variation in mineral concentrations are as follows.

E. A. McPherson, H. S. McTaggart, St C. S. Taylor and G. B. Young (unpublished) have shown genetic variation in Ca, Mg and P concentrations in an experiment with contemporary monozygotic and dizygotic twins on varying planes of nutrition.

Hansson (1948) and Hancock (1952) using monozygotic twins only (three pairs and nineteen pairs respectively) in greatly differing experimental situations agree, however, that variation between pairs was markedly greater than that within pairs for the concentrations of Ca and P. The same finding was made for Mg concentration studied by Hancock.

Payne *et al.* (1970), in the only non-twin work relevant here, have provided initial results on average Mg concentrations from one herd based on variable numbers of offspring of ten different bulls (from seven to twenty-three progeny per bull). The values for sire progeny groups ranged from 2·2 to 2·9 (mg/100 ml plasma) but no indication was given whether the variation among the sires was statistically significant or, if it were, whether it could be attributed to genetic differences. From other evidence on variation in blood Mg values and the numbers used, it seems unlikely that any but the extreme average values in this sample would differ significantly. Clearly, however, evidence of this type from larger numbers and a wider range of conditions will help to decide whether genetic variation for specific traits can be detected under field conditions and whether, when defined in this simple form it can be related to metabolic disorders and productivity.

Milk. Using monozygotic twins only, Hansson (1948) examined Ca and P concentration in three pairs; Comberg, Andreae & Meyer (1962–1963), the concentrations of Ca, P, Mg, Na and K in six pairs; and Field (1970*a*, 1970*b*), the concentration of Ca, Mg and K in three pairs. Again, in spite of the very different conditions of the three experiments, the results agree in showing much greater variation between than within pairs, implying a hereditary basis for the variation.

Excreta. Field & Suttle (1970) reported results from an experiment in which

dietary Mg and K were varied to study mineral interrelationships. Three pairs of monozygotic twins were used, but care was taken to ensure that the different pairs were of the same breed, age, physiological state and of similar weight. Values for urinary and faecal excretion of Mg, Ca, P, Na, and K showed that, in the urine, between-pair variation exceeded within-pair variation for Mg, Ca and, most markedly, for P; and in the faeces for Na and K. Since dietary Na and K are assumed to be completely available to the animal (Agricultural Research Council, 1965), the faecal losses can be equated with endogenous losses, and the results from the twins as evidence of genetic variation of Na and K in such losses.

The same study provided an indirect measure of the utilization of dietary Mg by the cows. The mean values for the three twin pairs were 22·8, 7·4 and 18·6% and differences within pairs were small.

Discussion

The evidence suggests that genetic variation exists both in the incidence of some disorders associated with mineral metabolism and in the concentrations of minerals in animal tissues and fluids. As yet, only a few of the minerals and even fewer of the trace elements essential to life have been investigated from this point of view. It is clear, however, that the large part of the variation among individual animals which was hitherto unaccounted for, should not be attributed wholly to chance.

Most of the reports on mineral concentrations in blood, with the possible exception of some of those on Cu, are concerned with variation in the apparently normal range (Underwood, 1962, 1966), although 'normality' itself is not necessarily the same for animals or for groups of animals that are different genetically. In many of the instances within this range, the genetic proportion of the total variation was found to be quite small. It does not follow, however, that the genetic fraction is negligible. Many of the other recognizable sources of variation – for example, the age or physiological state of an animal – are unalterable or cannot be modified in practice, and still other variation in mineral concentration has, as yet, completely unknown causes.

Underwood (1966) has stated that blood, in some aspect of its composition, invariably reflects the mineral status of an animal and often provides an early warning of deficiency, excess or imbalance. The question, therefore, arises whether genetically influenced variation in mineral status, as reflected by blood (or other fluids or tissues), is associated with genetically different needs of the animal. Does a breed with, for example, a genetically low average blood Cu concentration have a different requirement for dietary Cu from a breed with a genetically high average concentration? Is the one more prone to disorder than the other? For swayback there was clearly such an association but, more surprisingly, the evidence suggested that the concentration of Cu below which swayback occurred was itself influenced by heredity (Wiener, Field & Wood, 1969).

If genetic variation in requirements can be established, the nutritionist and veterinarian will have a more accurate means of assessing and of meeting require-

ments under those circumstances where the environment can be easily manipulated.

In this context it is interesting to note that Goldring, Schaible & Davidson (1940) reported a breed difference in the Mn requirement of laying hens and that Schwarz (1970) has recorded differences between genetically different strains of rats in the quantities of Se needed for a 50% protection against dietary liver necrosis.

Under other circumstances where the environment cannot be readily changed, it may be more appropriate to change the genotype. This could apply in vast areas of natural grazing across the world where mineral deficiencies and excesses would be very costly to rectify. It could also apply under intensive husbandry conditions where the provision of the appropriate feed may be prohibitively expensive. This might be argued, for example, in the provision of feeds sufficiently low in Cu to avoid poisoning in housed sheep and, in particular, those kept for breeding.

Another situation which might be met by genetic means is in producing animals with relatively stable concentrations of minerals in, for example, blood. This may be desirable if it reflects a lesser sensitivity (better physiological homeostasis) of the animal to adverse changes in the availability of, or requirements for, a mineral and if it involves factors which may not be readily controllable by husbandry. Only a little indirect evidence is available, as yet, of a genetic component of stability in Cu concentration. But a clue that a breeding policy aimed at achieving stability might be practical comes from the reported inverse association between average concentration and variability for Cu and Mg.

An important question relates to the magnitude of genotype-environment interactions which may be expected to occur. Is genetic variation in mineral status equally manifested under different environmental conditions and levels of nutrition? There is no direct experimental evidence on this point, and the indirect evidence is scant and equivocal. The absence of breed variation in an experiment with housed sheep fed on dry-lot in the USA, might be contrasted with the occurrence of breed variation for grazing sheep in experiments here and claimed as evidence for interaction. Equally, the different results may derive from the different breeds used. The marked breed differences for Cu concentration reported by Wiener and Field were almost certainly more important as a source of variation at all times of year than the reported interactions with season. But if the Cu results are thought to be specific to a farm situation with relative Cu deficiency there is no obvious evidence of nutritional deficiency of the other minerals for which genetic variation in concentration has also been reported.

The differences among minerals in their biological function, in their availability and in the way they are handled by the animal makes it contentious to generalize from one mineral to another. The present discussion should therefore be regarded mainly as an exploration of possibilities. The implications of genetic variation may well differ for different minerals.

The recognition of genetic variation in mineral metabolism, for which there is now some evidence for nearly every mineral where it has been sought, does not create any new problem for the nutritionist which did not already exist, but it is likely to provide an additional opportunity, in at least some circumstances, for

avoiding disorders due to mineral deficiency, excess or imbalance and perhaps for helping to optimize animal performance.

We are indebted to Mr W. S. Russell for the statistical analysis of the data on cattle blood leading to the results shown in Table 1.

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13

RELATIONSHIPS BETWEEN SWAYBACK INCIDENCE AND CONCENTRATION OF COPPER IN THE BLOOD OF SHEEP OF DIFFERENT BREEDS

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INTRODUCTION

Lambs affected by swayback (enzootic ataxia) generally have low Cu concentrations in their blood (Barlow, Purves, Butler and MacIntyre, 1960; Underwood, 1962). It has also been shown that ewes which had produced lambs affected by swayback, had lower Cu concentrations in their blood than contemporary ewes, which had produced normal lambs, when bled on a number of occasions between 9 and 27 months after the outbreak (Wiener, Field and Wood, 1969). It is not known, however, whether an outbreak of swayback has any lasting effect on the blood Cu levels of the flock in which it occurred. Two experimental flocks for which breed variation in swayback incidence and in blood Cu concentration have been reported (Wiener, 1966; Wiener, Field and Wood, 1969; Wiener and Field, 1971) were therefore examined for evidence that losses from swayback in a group of sheep leave the unaffected survivors as adults, with, on average, higher levels of Cu in their blood than sheep of corresponding groups in which swayback had not occurred or had occurred to a lesser extent. The data were also examined to see whether the occurrence of swayback affected subsequent breed comparisons in respect of blood copper levels.

MATERIALS AND METHODS

Flocks. The data from one of the two flocks studied comprised 311 ewes of the Scottish Blackface, Cheviot and Welsh Mountain breeds and the crosses among these breeds. They were born in the years 1960–64 at the farm of Blythbank, Peeblesshire. An outbreak of swayback occurred in 1964 when 90 of the sheep were born. These 90 were the survivors of 208 female lambs of which 34 had been lost from swayback in 1964 (a total of only 3 lambs were affected by swayback in the previous 4 years). Blood Cu levels were determined for 19th October 1965, 31st January 1966 and 7th June 1966.

The second flock, at Broughton Knowe, Peeblesshire, comprised 149 crossbred ewes derived from mating Scottish Blackface females to 3 or 4 rams of each of the 5 breeds: Border Leicester, Clun Forest, Dorset Horn, Finnish Landrace and Tasmanian Merino. Sixty-seven of the sheep were born in 1963 and 82 in 1964 (again the year when there was an outbreak of swayback). The 82 ewes were the survivors of 135 female lambs of which 16 were lost from swayback. The sheep were bled on August 1st, 1967 for determination of the copper concentrations.

In both flocks, each year in February (or March) from 1965 onward the ewes which had been mated in the preceding November or December were injected with a commercial preparation containing 50 mg. copper, in the form of copper calcium

edetate, in order to prevent further outbreaks of swayback. Possible effects of this treatment on the results will be discussed later. The sheep of both flocks were at grass all the year round with no separation of the breed groups. Other details of the management and structure of the flocks and the methods of copper determination were described by Wiener *et al.* (1969) and Wiener and Field (1971). The definition of swayback applied in these flocks was that described by Wiener (1966).

Method of calculation. The data for the Blythbank flock were restricted to the 311 ewes with complete records for each of the 3 occasions of bleeding and excluded those of the ewes born in 1960, 1961 and 1962 which had themselves produced swayback lambs in 1964. Such ewes had previously been shown to have had low blood Cu levels (Wiener *et al.*, 1969) and their inclusion would be liable to bias a comparison with the 1964-born group. By a process of "fitting constants" the data from both flocks were also adjusted for a number of other factors previously shown to contribute to variation in Cu levels (loc. cit.) and the average blood Cu level of each breed was calculated separately for the 1964-born sheep and for those born in earlier years.

For example, in the Blythbank flock in October 1965 the fitted mean value for the concentration of Cu in the blood of sheep born in 1964 was 74·5 μg./100 ml. and for the older sheep 75·5, i.e. an average difference (young minus old) of −1·0. Blackface sheep in the 1964 (young) group had a value of 57·4 and in the old group 55·3, i.e. a difference of 2·1 which was 3·1 μg. greater than the average difference. For Welsh sheep corresponding values were 87·5 in the young and 93·5 in the old group, a difference of −6·0, which was 5·0 μg. less than the average difference. It was then assumed that but for any effect of losses from swayback in 1964, which had varied markedly among the breeds, the deviations in Cu levels of the breeds from the average of their groups would be the same, within limits of sampling variation, in the 1964-born group and in the older group. To examine this point, differences in these breed deviations from the averages of their groups, i.e. the values of 3·1 for Blackface, −5·0 for Welsh, etc., were correlated with the corresponding swayback losses in each breed in 1964. In the Broughton Knowe flock a corresponding estimate from breed values was supplemented by a second estimate obtained from a comparison of rams. Two rams of each of the 5 breeds had left offspring in 1964, each ram with a differing incidence of swayback among his progeny. The difference in swayback incidence between the two rams of each breed was correlated with the corresponding difference in Cu level of the surviving progeny of each ram.

Losses of sheep from causes other than swayback and reasons for culling sheep surplus to experimental requirements were assumed to be unrelated to Cu levels.

RESULTS

Table 1 shows for each breed in each of the 2 flocks the proportion of female lambs lost from swayback (losses of male lambs are not considered here), the difference in blood Cu level between the sheep born in 1964, the year in which swayback occurred, and the sheep born in earlier years when none, or only negligible numbers were lost from swayback. Also shown are the correlations between the 2 sets of figures, weighted for numbers in the sub-classes. Swayback incidence varied from 0 to 41·4 per cent. depending on breed in the Blythbank flock and from 4·8 to 25·0 per cent. in the Broughton Knowe flock.

Except for June 1966, it can be seen from the positive correlation coefficients in Table 1 that the breed groups which had the highest incidences of swayback in 1964 showed the largest differences in Cu levels between ewes born in 1964 and ewes born in earlier years. For the Blythbank flock the highest coefficient arose

TABLE 1.

INCIDENCE OF SWAYBACK AMONG DIFFERENT BREEDS AND CROSSES

The correlation with the difference in blood Cu concentration (μg'/100 ml.) between sheep born in 1964 (when swayback losses occurred) and sheep born in earlier years (when no swayback occurred)

Blythbank flock							*Broughton Knowe flock*				
	Number of animals		*Swayback incidence*	*Difference in Cu levels**				*Number of animals*		*Swayback incidence*	*Diff. in Cu levels**
Breed or cross	*1964-born*	*1960-63 born*	*(%) in 1964*	*October 1965*	*January 1966*	*June 1966*	*Crosses of Scottish Blackface with:*	*1964-born*	*1963-born*	*% in 1964*	*August 1967*
Scottish Blackface (B)	7	19	41·4	3·1	12·0	0·9	Border Leicester	17	11	4·8	−0·8
Cheviot (C)	9	23	6·7	−2·5	1·0	3·5	Clun Forest	18	12	25·0	8·6
Welsh Mountain (W)	15	30	0·0	−5·0	−6·8	−0·2	Dorset Horn	16	14	6·7	5·1
B X C	19	39	20·8	5·2	2·2	−2·4	Finnish Landrace	18	20	12·1	−5·8
B X W	21	59	19·1	4·9	1·4	−3·2	Tasmanian Merino	13	10	5·3	−7·1
C X W	19	51	4·8	−5·7	−9·8	1·4					
Correlation of swayback incidence with Cu difference†				0·80	0·90	−0·13					0·53

* Cu levels in 1964-born sheep minus Cu levels in sheep born in previous years. Differences in Cu levels were calculated from breed values estimated separately in each group (see 'method of calculation' in text).

† Correlations weighted for numbers in sub-classes.

from the differences in Cu concentrations in January, that for October came next and for June there was a very low negative correlation. With the small number of pairs of observations available for calculating the correlations only the coefficient for January was significant at the 5 per cent. level of probability and that for October came close. The differences among the estimates from the different times of the year conform to expectation and will be discussed later. The corresponding correlation coefficient for the Broughton Knowe flock, bled in August, was 0·53 and the estimate (not shown in the Table) independently derived from differences in swayback incidence and in Cu values of ram progeny groups within breeds was 0·73.

DISCUSSION

The results suggest that swayback losses removed lambs with low (below average) Cu levels in each group—which might have been expected on the general grounds that swayback is associated with a low Cu status of the animal (Barlow *et al.*, 1960; Underwood, 1962). That the consequences of this selection in respect of Cu levels then persisted into adulthood is reflected by the relatively high Cu levels of the survivors, which had apparently been unaffected by swayback themselves although existing in an environment which would favour its occurrence.

Consideration must, however, be given to the possibility that breed differences in the sheep born in 1964 might not have been the same as among those born in earlier years even without an outbreak of swayback in 1964. In the Blythbank flock the ewes born in 1963 or earlier, but not those born in 1964, had received a prophylactic injection of copper in February 1965. Whether for this reason, in spite of some evidence against long-term residual effects of Cu injection (Butler and Barlow, 1963), or because of an age effect on Cu level, as suggested by Wiener *et al.* (1969), the 1964-born group had lower Cu levels than the older sheep by, on average, 1, 8 and 2 μg./100 ml. blood in October 1965, January 1966 and June 1966 respectively. In the Broughton Knowe flock, the 1964-born ewes had on average 6 μg. less Cu per 100 ml. blood than the 1963-born, when bled in August 1967. In this flock, however, both groups had received a prophylactic copper injection in 1966 and 1967 (but only the older group in 1965).

Wiener *et al.* (1970) have noted a tendency in the Blythbank flock for breed variation in Cu levels to be greater when average levels for the flock were low than when they were higher. At low average levels, as for example in January, the breeds at the low end of the scale tended to be even lower relative to breeds at the top end. If this trend were present in these data it would work in the opposite direction to the results actually observed. Thus the effect of swayback losses in removing sheep with low Cu levels might well have been underestimated. The exclusion of the older ewes known to have produced swayback lambs would also tend to diminish any differences between Cu levels of the 1964-born and the older sheep. The correlation between swayback incidence and Cu levels estimated from differences between ram progeny groups in the Broughton Knowe flock is free from the above complications since only the sheep born in 1964 were concerned. It may be inferred from the present results that, but for the swayback losses, females born in 1964 in the Blythbank flock would have had

even lower Cu levels relative to older ewes than reported by Wiener *et al.* (1969).

The probability of producing swayback has been shown to be subject to genetic variation (Wiener, 1966; Wiener and Sampford, 1969). Lambs which were unaffected in a year when others were lost through swayback may, therefore, be assumed to be less prone as adults to produce swayback lambs in their turn. In practice, the benefits of such natural selection might be difficult to detect because prophylactic measures intended to curb swayback and the purchase of rams, for example, from unaffected flocks would counteract any selection against the disease by maintaining susceptible sheep in the breeding population.

The present results, however, pose the question whether artificial selection for Cu levels, without the intervention of swayback, would lower swayback incidence. The effectiveness of this would depend on the magnitude of the genetic correlation between Cu levels and swayback incidence, for which no estimate is available. However, breed differences in Cu levels were highly correlated (between $-0{\cdot}8$ and $-0{\cdot}9$) with corresponding breed differences in swayback incidence, using the results of Wiener (1966) for swayback incidence and of Wiener *et al.* (1969) for Cu levels, which suggests that some of this relationship arises from a common inheritance. Combined evidence from a variety of sources (Butler and Barlow, 1963; Suttle and Field, 1969; Wiener and Field, 1969) suggests, however, that the relationship of blood Cu level to swayback incidence is not simple. Therefore, selection for blood Cu levels alone might show a variable response in different groups of sheep in terms of swayback incidence.

The present results suggest, however, that among adult sheep selection at some periods of the year, when correlations were strong, would be more effective than selection at others. The "selection" by swayback losses resulted in a large difference in January Cu levels, no difference in June levels and an intermediate difference in October levels. This agrees well with a corresponding seasonal pattern found in the difference in blood Cu levels between ewes which had produced swayback lambs and those which had produced only normal lambs in the same year. These differences were large in January, absent in June and intermediate in October (Wiener *et al.*, 1969).

It follows from the present results that estimates of genetic variation in Cu levels when based on survivors of an outbreak of swayback are likely to differ from estimates based on a population in which swayback had not occurred, either naturally or because it was prevented. In the present experiments, breed variation was not significant in the "selected" groups, but much more pronounced, and significant, in the "unselected" populations.

SUMMARY

In 2 flocks of sheep each comprising several breeds which had suffered differing losses from swayback in 1964, a comparison of blood Cu levels of ewes born in the swayback year and others born in years when swayback had not occurred suggested that swayback had removed the lambs with lower than average Cu levels, and that the consequences of this persisted into adulthood. The unaffected survivors as a group had a correspondingly higher average level of Cu in their blood.

Differences in average Cu level between the ewes born in the swayback year and the otherwise comparable ewes born in non-swayback years were greater the higher the incidence of swayback losses associated with them. This effect was more marked in winter than in summer, following a prophylactic Cu injection in February. The correlation coefficients, quantifying this relationship, were 0·80 (October 1965), 0·90 (January 1966) and −0·13 (June 1966). For the second flock bled once in August 1967 independent estimates of the corresponding correlation coefficient were 0·53 and 0·73.

The results are discussed in relation to selection against swayback.

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VARIATION IN THE CONCENTRATION OF COPPER IN THE BLOOD PLASMA OF FINNISH LANDRACE AND MERINO SHEEP AND THEIR CROSSES WITH REFERENCE TO REPRODUCTIVE PERFORMANCE AND AGE

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SUMMARY

Concentrations of copper in blood plasma were determined in January and in February 1971 and in February and March 1972 in a grassland flock of sheep comprising the Finnish Landrace and (Tasmanian) Merino breeds and their reciprocal crosses. Numbers of animals ranged from 30 to 100. The unadjusted mean copper levels of the flock varied from 63 to 81 μg/100 ml. The Finnish Landrace had a markedly lower plasma copper concentration than did the Merino, the mean difference after adjustment for other factors varied from 16 to 54 μg/100 ml. First crosses had levels halfway between those of the parental breeds. Copper concentration fell in the 4-week period between February and March 1972 when most of the ewes were pregnant. This fall was greatest for the Finnish Landrace which started with the lowest level and least for the Merino.

Neither the breed differences in the change in level nor the actual concentration appeared to be related to the number of lambs (0 to 4) carried by the ewes. Variation in copper level associated with the age of ewe, significant for the two bleedings in 1972, was largely attributable to the higher level among the youngest age class, approximately 10 months old when bled. The stage of pregnancy at the time of blood sampling, as reflected by date of lambing, did not significantly affect plasma copper concentration in this flock.

INTRODUCTION

BREED differences in the concentration of copper in the blood of sheep, first demonstrated by Wiener and Field (1966) and subsequently supported by results from two separate flocks (Wiener, Field and Wood, 1969; Wiener and Field, 1971a) are of particular interest if they can be shown to indicate differences in the requirements of these breeds for dietary copper—reflected in extreme cases by the occurrence of disorders associated with copper metabolism. Breed differences in such disorders have been reported by Wiener (1966) and Poole (1970) for the incidence of swayback and by Lüke

and Wiemann (1970) and Wiener and Macleod (1970) in relation to copper poisoning. Previous work had also shown that changes in blood copper level from one sampling to the next was found to vary with breed (Wiener, Field and Jolly, 1970) the changes being, in general, greatest for the breed with the lowest copper value. A further finding from the earlier results was that copper levels in whole blood of crossbred sheep tended towards, and in some cases exceeded, those of the parent breed with the higher concentration.

The present experiment gave the opportunity to examine variation in copper levels of blood plasma for two breeds, the Finnish Landrace and Tasmanian Merino, not previously studied for this trait in the pure breeds and to examine its inheritance in crosses. The availability of reciprocal crosses between these breeds also permitted study of the possibility that maternal effects persist into adulthood. Further, this flock, because of a range in litter size from 0 to 4, seemed particularly suitable to examine the effect of litter size on copper levels of pregnant ewes.

MATERIAL AND METHODS

Animals and management

Copper determinations were carried out on sheep involved in an experiment started by Drs H. P. Donald and R. B. Land to study reproductive performance in a flock of Finnish Landrace and Tasmanian Merino sheep and the reciprocal crosses between these breeds maintained as a single grassland flock from 1968 to the autumn of 1970 at the Animal Breeding Research Organisation's farm of Dryden Mains and subsequently at Blythbank in Peeblesshire. The foundation animals for this experiment were derived from the Finnish Landrace flock at Blythbank built up from an importation in 1962 (*see* Donald and Read, 1967) and from the Merino flock at Dryden bred from an importation in 1955. Until 1968, when sheep of both breeds were brought together for the present experiment, they had been treated slightly differently at their respective locations, the most apparent difference being that Finnish Landrace ewes were housed for 2 weeks prior to lambing and for 6 to 8 weeks thereafter whilst the Merinos were housed at lambing for a few days only. From 1968 on, all females were treated alike, as a grassland flock, and housed for a few days at lambing. The foundation females were mated each year to two rams of each breed, Finnish Landrace and Merino (using different rams every year) to produce purebred and crossbred progeny whilst these offspring (hereafter referred to as the 'experimental' generation) were mated to Welsh Mountain rams. Females were mated so as to lamb for the first time at 1 year old.

On 3 March 1971 all females were dosed orally with a solution containing 0·75 g of copper sulphate since the low plasma copper values estimated on a sample of the flock had indicated the advisability of a prophylactic treatment. No copper treatments had been given before or since that time in this flock. No swayback was recorded among the lambs of this flock in any year.

Blood sampling and copper estimation

Blood samples were taken from females between the ages of 10 months and 7 years old on four separate occasions, (1) 18 January 1971 on a sample of 30 of the experimental animals, 10 picked at random from each of the two

pure breeds and 10 from the crossbreds. (2) 17 February 1971 when the whole flock including the foundation ewes was bled. (3) 3 February 1972 when the whole flock was bled (this time including the animals born in 1971) and (4) 3 March 1972, again the entire flock. Copper concentrations were determined in plasma by a colorimetric method (Summers, 1960) for the first two occasions (1971) and by atomic absorption for the last two (1972). The methods of collecting the blood and of copper estimation by atomic absorption, were as described by Wiener and Field (1971a).

Statistical analysis

A least squares analysis was used with parameters representing the effects of breed, source of animal, age of ewe, lambing performance and lambing date. The data were unsuitable for direct calculation of interactions between breed and lambing performance.

TABLE 1

Unadjusted flock and breed means for the concentration of copper in blood plasma (μg/100 ml) on four occasions

	January 1971			February 1971			February 1972			March 1972		
	No.	Mean Cu	SE	No.	Mean Cu	SE	No.	Mean Cu	SE	No.	Mean Cu	SE
Flock	30	81·0	4·0	76	66·8	3·2	100	70·1	2·7	100	63·0	3·0
Merino	10	91·3	7·2	28	81·6	4·8	32	90·0	3·6	32	87·6	3·9
Finnish Landrace	10	67·6	7·6	30	50·3	5·0	38	47·5	3·2	38	37·2	3·5
Finnish Landrace × Merino†	10	84·0	7·6	18	71·4	3·9	30	77·6	3·8	30	69·4	4·0

† Crossbred values are for the pooled reciprocal crosses.

Correlations were calculated between plasma copper values obtained at different times thus giving some measure of the repeatability of the observations. Two sets of correlations were examined; the total correlation and the residual correlation after variation attributable to the common effects such as breed, age etc. had been accounted for (as described by Wiener and Field, 1969a).

RESULTS

The first Table shows the unadjusted means for each of the four occasions of sampling and separately for each of the two breeds and the crosses among them. It was on the basis of the apparently large and significant breed differences at the first sample bleeding in January 1971 that the subsequent work was initiated. The preliminary results in Table 1 also indicate strongly that the crossbred sheep had levels of copper in their blood plasma approximately halfway between the levels of the pure breeds.

Subsequent statistical analysis took simultaneous account of the factors referred to earlier as possible sources of variation.

Variation attributable to environmental differences associated with the different groups of sheep (foundation Finnish Landrace, foundation Merino, and experimental generation) was found to be non-significant but possibly too large to be ignored; the parameters were therefore retained in the analysis.

Differences in copper levels between the reciprocal crosses born within the experiment were negligible (Table 2) and suggested that by the time the

TABLE 2

The effect of maternal breed on blood copper levels (μg/100 ml)

Sire breed	Dam breed	February 1971 No.	February 1971 Fitted value†	February 1971 SE‡	February 1972 No.	February 1972 Fitted value†	February 1972 SE‡	March 1972 No.	March 1972 Fitted value	March 1972 SE‡
Finnish Landrace	Merino	7	71·6	13·3	13	71·2	7·1	13	62·3	8·2
Merino	Finnish L.	11	66·8	—	17	71·2	—	17	60·1	—

† Fitted values for 1-year-old barren females.
‡ Standard error of the difference between the reciprocal crosses.

crossbred animals were between 10 months and 3 years old, it mattered not whether they had been born to Finnish Landrace or Merino mothers. Data from the reciprocal crosses were therefore pooled in subsequent analyses.

Tables 3 and 4 show the adjusted breed values for the Merino and the Finnish Landrace and the crossbreds. The analysis was done throughout in two parts, the first for animals present both in February 1971 and in February 1972 (Table 3) and the second for those present in February

TABLE 3

The effect of breed on blood copper levels (μg/100 ml) for females present both in 1971 and 1972

Breed	No.	February 1971 Fitted value†	February 1971 SE‡	February 1972 Fitted value†	February 1972 SE‡
Merino	28	76·9	—	93·2	—
Finnish Landrace	30	60·6	18·6	63·1	13·5
Finnish Landrace × Merino §	18	69·4	15·3	76·7	11·1

† Fitted values are for females 1 year old in 1971 which were barren in both years.
‡ Standard errors apply to deviations from Merino.
§ Crossbred values are for the pooled reciprocal crosses.

and March 1972 (Table 4). Standard errors, given for the differences from Merino, are high on account of a very unequal distribution of breeds at the subclass level. Breed differences showed the same ranking on all occasions; the variation attributable to breed was significant only for the larger sample of animals of the 1972 data (determined by atomic absorption) when Finnish Landrace sheep were found to have less than half the copper concentrations in their plasma of those of their Merino contemporaries. Crossbred sheep are seen to have plasma copper concentrations almost exactly midway between the levels of their parental breeds.

TABLE 4

The effect of breed on blood copper levels (μg/100 ml) for females present in February and March 1972

		February 1972		March 1972		Proportionate difference†	
	No.	Fitted value‡	SE§	Fitted value‡	SE§	Fitted value‡	SE§
Merino	32	96·1	—	90·4	—	0·13	—
Finnish Landrace	38	46·6	7·9	35·9	9·2	0·39	0·11
Finnish Landrace × Merino‖	30	71·2	7·1	61·6	8·2	0·26	0·10

† The proportionate difference between the February and March copper levels was calculated as: (February–March)/February for each animal.

‡ Fitted values are for barren females 1 year old in 1972.

§ Standard errors apply to deviations from Merino.

‖ Crossbred values are for the pooled reciprocal crosses.

A further interesting point arising from Table 4 shows that the fall in plasma copper level between February and March 1972 was greater in the Finnish Landrace which started with the lowest average level and least in the Merino which started with the highest. The proportionate change shown in the last column was statistically significant.

The results in Table 5 show that variation in copper levels attributable to lamb numbers was non-significant and there was no obvious trend attributable to pregnancy and lamb numbers. Proportionate changes in copper values between February and March 1972 were statistically significant ($P < 0{\cdot}05$) but there was no evidence that over this 4-week period of pregnancy the drop in copper levels was related to litter size or to the starting level.

It was noted that within breeds there were no significant differences between pregnant and barren sheep and between sheep carrying above and below average numbers of lambs. It is inferred from this that interactions involving these factors are unlikely to have been important in this experiment.

TABLE 5

The effect of number of lambs born on blood copper levels (μg/100 ml) for the three main sampling occasions and on changes in levels between February and March 1972

	February 1971			February 1972			March 1972		Proportionate difference†	
No. born	No.	Fitted value‡	SE§	No.	Fitted value‡	SE§	Fitted value‡	SE§	Fitted value‡	SE§
Zero	13	76·9	—	24	96·1	—	90·4	—	0·13	—
One	29	+14·4	12·2	31	−1·4	7·6	−2·1	8·8	−0·03	0·11
Two	21	+7·3	16·5	26	+7·4	9·8	+12·8	11·3	−0·21	0·14
Three	10	−3·8	20·0	17	+15·0	11·6	+16·9	13·4	−0·19	0·16
Four	3	+16·4	23·4	2	+8·4	16·8	−4·5	19·4	+0·29	0·23

† The proportionate difference between the February and March copper levels were calculated as: (February–March)/February for each animal.

‡ Fitted values are for 1-year-old Merinos having no lambs, values for one or more lambs are given as deviations from this.

§ Standard errors apply to deviations from zero born.

Lambing dates were spread over a period of approximately 6 weeks and ewes, when bled, were consequently at different stages of pregnancy. This, however, does not appear to have contributed significantly to variation in plasma copper levels and there was no consistent trend associated with date of lambing.

The effect of age on plasma copper concentration could not be clearly assessed since the foundation groups of ewes were from 3 to 6 years old in

TABLE 6

The effect of age on blood copper level (μg/100 ml) in two groups of sheep and two years

Origin of females: experimental flock†

		Age (years)		
		1	2	3
1971 February	Number	23	18	—
	Fitted value‡	79·3	−14·6	—
	SE§	—	10·1	—
1972 February	Number	25	22	18
	Fitted value‡	111·7	−32·0	−26·0
	SE§	—	7·1	7·4
March	Fitted value‡	102·1	−30·3	−21·5
	SE§	—	8·2	8·5

Origin of females: foundation flock†

		Age (years)				
		3	4	5	6	7
1971 February	Number	5	14	9	7	—
	Fitted value‡	67·7	−1·9	−12·7	−5·4	—
	SE§	—	20·8	21·0	19·8	—
1972 February	Number	—	5	14	9	7
	Fitted value‡	—	92·9	−7·2	−29·1	−18·0
	SE§	—	—	11·1	12·3	11·6
March	Fitted value‡	—	80·1	−2·8	−12·2	−15·0
	SE§	—	—	12·8	14·2	13·5

† See text.

‡ Fitted values are given in terms of barren Merino females and the youngest age class within each group of sheep. Values for older sheep are given as deviations from the appropriate base.

§ SE apply to deviations from the appropriate age class.

1971, and from 4 to 7 years old in 1972, whilst the sheep born within the experiment were younger. Age variation, therefore, had to be analysed separately within each of these two groups of sheep. Results are shown in Table 6. The most marked effect found was that the sheep sampled prior to their first birthday had higher levels of copper in their blood plasma than older sheep. As an average effect, age variation was significant both in February and March 1972. The possible influence of changes in management on these results will be discussed later.

The residual correlation (corresponding to a correlation within subclasses) between the copper values obtained in February of successive years (involving copper determinations by two different methods) was 0·51 and highly significant. The corresponding correlation between the copper values in February and March 1972 (both determined by the same method) was 0·71 ($P < 0·001$).

DISCUSSION

Relationships to pregnancy

Since the Merino sheep involved in the present experiment had typically fewer lambs at birth than the Finnish Landrace ewes but markedly higher levels of copper in their blood plasma when the two breeds were run together as a single flock, copper level appeared superficially to be negatively related to lamb numbers. Also, Wiener, Field and Wood (1969) had found that barren ewes had higher levels of copper in whole blood than those carrying lambs and that, on average, ewes giving birth to twins had slightly lower levels than those giving birth to singles (although interactions with breed were also recorded). Statistical analysis of the present results, showed, however, that when other factors, including breed, were held 'constant', there was no clear or significant relationship between the level of copper in the plasma of blood sampled in early February or March and the number of lambs subsequently born, varying from 0 to 4, during the lambing period from approximately mid-March to early May. In addition, there was no significant difference in either copper values or changes in copper values when barren and pregnant sheep were compared. Hence, the observed fall in plasma copper values from February to March 1972 cannot simply be attributed to pregnancy but may involve possible seasonal changes. However, the possibility that pregnancy influenced the observed changes in copper levels cannot be ruled out either, because the unequal distribution of barren sheep among the breed and age classes and some particularly low copper levels among the few barren Finnish Landrace sheep suggests that the evidence from the barren sheep may not be trustworthy.

In the present experiment there was a tendency for the groups of sheep with the higher copper status (i.e. Merino) to have dropped less in copper level than the Finnish Landrace with an already lower level, whilst the Finnish Landrace × Merino crossbreds occupied an intermediate position. This is in agreement with the findings of Wiener, Field and Jolly (1970) who suggested that sheep with high blood copper levels may be in some way more buffered from changes in copper requirements or copper availability, although the effects may be mediated by copper levels in the liver.

Age effects

Age effects were particularly marked in 1972 when the sheep then sampled for the first time had been born at Blythbank to mothers which had themselves received a dose of copper sulphate during pregnancy. The older sheep had been born at Dryden. It is difficult to imagine, however, why these young sheep should, by virtue of the treatment of their mothers, have higher levels than the mothers themselves which had been the direct recipients of the copper supplementation. The general trend of having higher copper levels amongst the younger sheep was, however, also apparent in 1971 when there were no management differences to add a possible complication to the interpretation

of the results. Evidence on age trends from the literature gives limited support to these results. Eden (1939) found that 1-year-old sheep tended to have distinctly higher copper values than older sheep, whilst Wiener *et al.* (1969) found, in general, no significant variation among ages of ewes from 2 years old and over.

Genetic effects

The marked breed variation observed in the present experiment supports the general finding reviewed by Wiener and Field (1971b) that the concentration of certain minerals in the blood, and copper in particular, is subject to genetic variation. In relation to these particular breeds it also reinforces the relative ranking of the Merino and the Finnish Landrace (albeit with rams from the same original importations) when used in a crossbreeding experiment reported by Wiener and Field (1971a). A discrepancy arises from the fact that in the present experiment crossbred sheep were halfway in their copper levels between those of their parent breeds suggesting that genetic variation was additive, whereas in the work previously described by Wiener *et al.* (1969) in which Scottish Blackface, Cheviot and Welsh Mountain breeds were involved, the crosses tended to have copper levels at, or occasionally above those of the parent breed with the higher level, suggesting that non-additive genetic variation is likely to be important. Differences between the two flocks therefore require some examination to see whether they might explain the apparently different modes of inheritance of copper concentrations which have been inferred.

The earlier study (Wiener *et al.*, 1969) was based on copper in whole blood and the present study on copper in blood plasma. Comparable differences among breeds and crosses (unpublished) to those in the published results for whole blood copper had, however, also been noted for plasma copper in samples of sheep from later generations in the same flock. Also in general, copper estimations from whole blood and from plasma are thought to be closely correlated (Underwood, 1971). The point, however, requires further investigation in the genetic context.

The two flocks involved differed in the environmental conditions provided for the sheep. Whilst this may lead to a difference in the manifestation of genetic variation, some explanation would still be required why crossbreds, run with the purebreds, should have responded differentially.

The breeding systems were different in the two flocks. First crosses (F_1) were involved in the present, Finn-Merino, experiment, whilst in the earlier study the crosses were of F_2 and subsequent inbred generations (crosses mated among themselves). If the deviation of crossbreds from the mean of the parental breeds is due to non-additive action of genes, an F_1 group should, on theoretical grounds, show a greater deviation than subsequent crossbred generations—the opposite trend to that observed when comparing the two experiments. On the other hand, if natural selection had favoured high copper levels the opportunities for this to occur would be expected to have been greater in the crossbred animals of the first flock studied because of gene segregation in F_2 and subsequent generations. Re-examination of the original data, however, provided no indication that the crossbred deviation had arisen in this way.

The breeds differed in the two flocks under discussion. Frequencies of the genes controlling blood copper levels may differ among breeds such that

a variety of genetic models could account for the observed results. The possibility that the inheritance of blood copper levels is further mitigated by genetic variation in liver copper concentrations (Wiener and Field, 1969b) adds a further complexity. No resolution of this problem seems possible, therefore, without further breeding experiments preferably involving all five breeds. The geographically different origins of these breeds and the typically different conditions under which they were developed and historically used, makes it plausible that they have been subjected to different selection pressures for copper uptake and requirements and that this in turn may account for different gene frequencies in the present populations of these breeds.

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AN ASSOCIATION BETWEEN THE CONCENTRATION OF COPPER IN WHOLE BLOOD AND HAEMOGLOBIN TYPE IN SHEEP

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SUMMARY

In a genetically diverse flock of about 320 sheep a significant association has been found between the concentration of copper in whole blood and the haemoglobin type.

Sheep were bled on four occasions over a period of 1 year, with the flock mean concentration of copper varying between 53 and 96 μg per 100 ml whole blood. The copper concentrations in whole blood from sheep of haemoglobin type B exceeded those from sheep of type A by 9, 16, 15 and 15 μg per 100 ml on the four occasions respectively. The copper concentrations from sheep of type AB were 8, 11, 7 and 7 μg higher than those from type A.

Differences in the frequency of the three haemoglobin phenotypes accounted for part of the breed variation in copper concentration previously observed in the same flock, but even when that effect was allowed for, highly significant breed variation remained.

When plasma instead of whole blood was examined in two other flocks from which breed variation in plasma copper concentration had been reported no association was found between the plasma copper concentration and haemoglobin type.

INTRODUCTION

PREVIOUS studies have shown marked breed variation in the concentration of copper in the blood of sheep. One of these studies was concerned with copper in whole blood (Wiener, Field and Wood, 1969), whilst two others were concerned with copper in the plasma (Wiener and Field, 1971; Hayter, Wiener and Field, 1973).

The normal haemoglobin types differ in frequency among breeds and are associated with the concentration of some red cell constituents (*see* Agar, Evans and Roberts, 1972). These associations also apply to the flocks of this study (Hall and Hunter, 1973).

Comparing the published data on the frequency of the haemoglobin type alleles in different breeds with the comparable published data on copper concentration shows a crude relationship such that the higher the frequency of type A the lower the copper concentration. If substantiated, it could explain some of the previously recorded breed variation in copper concentration and might elucidate some of the differences noted (*see* Hayter *et al.*, 1973) in the variation attributable to crossbreeding when results from

whole blood copper in one flock were compared with those from plasma copper in another flock.

This paper gives the results of re-examining the copper concentrations of the blood of sheep of three flocks in relation to individual haemoglobin types.

MATERIAL AND METHODS

Each of the three grassland flocks involved in this study comprised several breeds and breed crosses of sheep which were run together and managed alike. The animals, the management and the methods of determining copper have been described in some detail in previous publications; essential points are as follows:

Flock 1—comprising the Scottish Blackface, Cheviot and the Welsh Mountain breeds and the crosses among these breeds. Sheep were bled on four separate occasions at different seasons of the year. Copper was determined on whole blood (Wiener *et al.*, 1969).

Flock 2—comprising the adult females derived from crosses of Scottish Blackface females mated to rams of the Border Leicester, Clun Forest, Dorset Horn, Finnish Landrace and Tasmanian Merino breeds. (The haemoglobin types were not determined for the lambs in this flock on which copper concentration had also previously been reported.) Sheep were bled on one occasion in August 1966. Copper was determined on the blood plasma (Wiener and Field, 1971).

Flock 3—comprising the Finnish Landrace and Tasmanian Merino breeds and their reciprocal crosses. Sheep were bled on three occasions in successive winters. Copper was determined on blood plasma using a colorimetric method for the first occasion and atomic absorption for the last two (Hayter *et al.*, 1973).

The haemoglobin types were determined by electrophoresis at pH 8·6, 6 volts per cm on Connaught starch gel (buffer of Tris (hydroxymethyl) methylamine 40·4 g, diamino ethane tetra acetic acid 4·0 g, boric acid 3·0 g, distilled water 2 litre) or Whatman's No. 17 paper (buffer of A = sodium borate 19·1 g, distilled water 1 litre; B = boric acid 12·4 g, sodium chloride 2·93 g, distilled water 1 litre. Mix equal parts of A and B, adjust to pH 8·6 by adding A or B).

Statistical analysis. A least squares analysis was used with parameters representing the effects of breed, haemoglobin type, and other factors, such as age of animal, lambing performance and lambing date, which were found in previous studies to have significantly affected variation in copper concentration at some stage. Fitted means for each flock were expressed in terms of adult sheep of haemoglobin type A which had produced lambs in an average week of lambing and of the breeds appropriate to each flock. A few aspects of management found to have affected copper concentrations were, however, peculiar to flocks. Hence a slightly different statistical model had to be applied to the data from each flock (though not to different bleedings within a flock) in order to provide the necessary comparisons among haemoglobin types and breeds within flocks. In the absence of a fully satisfactory fitted base line from which to compare the flocks with each other, apart from their breed differences, the unadjusted flock averages are given as a guide to the prevalent copper levels.

Only the animals on which information on both copper and haemoglobin

types was available were included in the analysis. This number is slightly smaller than those included in the published results on copper alone.

In respect of flock 1 the analysis was done in two parts, the first on the animals present on each of the last three occasions of bleeding (October 1965, January 1966 and June 1966) and the second on all sheep present in the summer of 1965. This sample differs in that it does not include the youngest age class of sheep bled for the first time in October 1965 (88 animals) but does include 29 more animals of the oldest age group not present on later occasions.

For flock 2 only one bleeding, in August 1966, was involved and for flock 3, again the analysis was done in two parts, the first for animals present in February 1971 and a second analysis for a larger number of animals in common to February 1972 and March 1972.

RESULTS

Table 1 shows the unadjusted mean copper concentration of whole blood of sheep in flock 1 on four occasions and the deviations from the fitted flock

TABLE 1

Flock 1. Copper concentration in whole blood of sheep (μg/100 ml) in relation to haemoglobin type on four occasions

	Summer 1965			Oct. 1965			Jan. 1966		June 1966	
	No.	Mean	SE	No.§	Mean	SE	Mean	SE	Mean	SE
Unadjusted flock mean	265	96·6	1·3	324	77·1	1·6	53·1	1·5	79·6	1·5
Fitted flock mean†	265	74·6	—	324	49·3	—	35·2	—	50·6	—
Deviations for Hb type										
A	61	0·0	—	72	0·0	—	0·0	—	0·0	—
AB	109	7·9	3·5‡	135	10·6	4·3	7·4	3·9	7·2	3·9
B	95	8·9	3·8	117	15·8	4·5	15·4	4·1	15·7	4·1

† Fitted mean in terms of Scottish Blackface sheep.
‡ SE for deviation from HB type A.
§ Number present on the three occasions October 1965, January 1966 and June 1966.

mean (expressed in relation to the Scottish Blackface breed) attributable to haemoglobin type when other factors were held constant. It can be seen that the haemoglobin type AB was associated with a higher level of copper than type A and that the type B was associated with a higher level still. It appears that each substitution of the B allele for the A allele increased copper concentration by approximately 7 to 8 μg of copper per 100 ml whole blood. Variation in copper concentration attributable to haemoglobin type was statistically highly significant ($P<0·01$) for the last three occasions shown and significant at $P<0·05$ for the summer of 1965. The fact that the B type differed only a little from the AB type in the summer of 1965 detracts from the impression brought out by Figure 1 that the differences attributable to haemoglobin type were approximately the same at differing times of year in spite of differing flock means.

The breeds and crosses involved in flock 1 differed in the frequency of the haemoglobin alleles as shown in Table 2. The Blackface breed had the highest frequency of the A allele and among the pure breeds the Cheviot had

the lowest. The crossbreds had a lower frequency of the A allele (and a correspondingly higher frequency of the B allele) than might have been expected from the frequencies in the pure breeds. In view of the differences of copper concentrations associated with haemoglobin type, a part of the

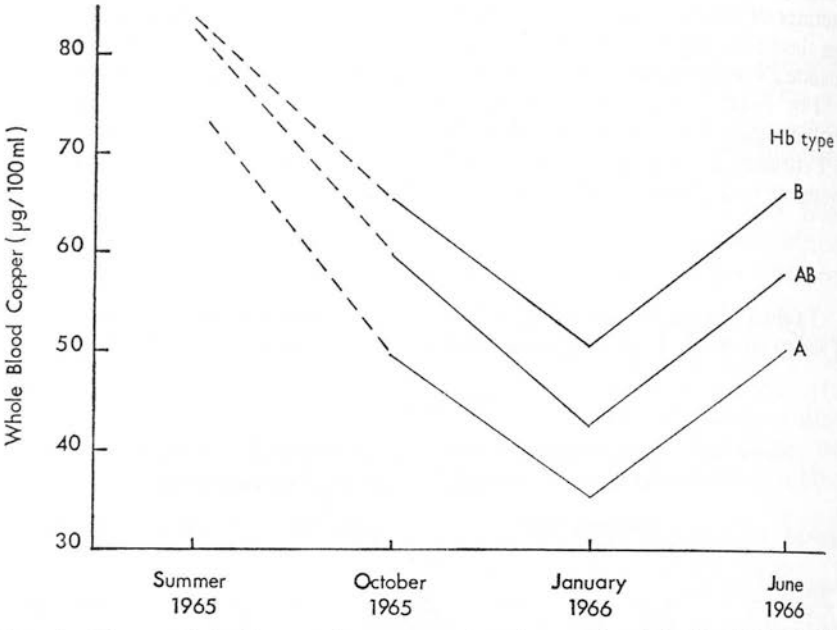

FIG. 1. The association between the concentration of copper in whole blood (fitted values) of sheep on four occasions and haemoglobin type (Flock 1).

TABLE 2

Flock 1. Fitted values for copper concentration in whole blood of sheep of different breeds (µg/100 ml) when: (1) Hb *type held constant; (2)* Hb *type ignored*

		No.	Freq. of A allele	Summer 1965 Mean	SE†	No.‡	Freq. of A allele	Oct. 1965 Mean	SE	Jan. 1966 Mean	SE	June 196 Mean
Breeds												
Blackface	1	30	0·87	74·6	—	34	0·85	49·2	—	35·2	—	50·2
	2			77·6	—			53·4	—	38·4	—	53·4
Cheviot	1	27	0·22	73·7	5·8	31	0·22	53·5	7·2	37·6	6·6	60·5
	2			82·2	5·4			67·3	6·8	49·9	6·2	72·9
Welsh	1	35	0·37	84·4	5·5	44	0·41	81·5	6·7	55·0	6·1	74·4
	2			92·1	5·2			93·0	6·4	64·8	5·9	84·2
Blackface/Cheviot	1	52	0·41	78·6	4·9	64	0·39	60·9	6·0	49·9	5·5	64·5
	2			86·0	4·6			72·5	5·7	60·0	5·3	74·7
Blackface/Welsh	1	66	0·54	89·8	4·8	81	0·52	69·9	5·9	52·5	5·4	72·4
	2			96·4	4·6			80·2	5·7	60·4	5·2	80·2
Cheviot/Welsh	1	55	0·25	89·8	5·2	70	0·26	71·7	6·3	50·6	5·8	74·7
	2			98·4	4·7			85·3	5·8	62·5	5·3	86·6

† SE for deviation from Blackface.
‡ No. present on three occasions.

breed differences and a part of the differences between the crosses and pure-breds can be explained in terms of the differing frequencies of the haemoglobin alleles in the different groups. This is shown in Table 2 where the copper concentrations of the different breeds and crosses are shown as

deviations from the Blackface, first when haemoglobin type was held constant in the statistical analysis, and secondly when haemoglobin type was ignored. The variation attributable to breed represented approximately 10% of the total variation when haemoglobin type was ignored, when, in other words, variation in haemoglobin type was regarded as a component of breed differences. Variation attributable to breeds was somewhat lower (approximately 7%) when haemoglobin type was held constant. In both cases, however, breed variation was statistically highly significant ($P<0.001$). When haemoglobin type was held constant the values for the crossbred groups of sheep were still markedly higher than the mid-parental values, although not to quite the extent reported previously.

Table 3 shows that when copper was determined in blood plasma in two other flocks of sheep there were no associations with haemoglobin type although all three types were represented in the flocks concerned. Taken at

TABLE 3

Copper concentrations in blood plasma of sheep (μg/100 ml) in flocks 2 and 3, in relation to haemoglobin type

		Flock 2			*Flock* 3							
		No. of sheep	August 1966 Mean	SE	No. of sheep	Feb. 1971 Mean	SE	No. of sheep§	Feb. 1972 Mean	SE	March 1972 Mean	SE
Unadjusted flock mean		150	105·7	3·0	69	66·5	3·4	94	70·3	2·9	63·0	3·1
Fitted flock mean†		150	93·6	—	69	75·3	—	94	84·1	—	82·5	—
Deviations for Hb type:	A	35	0·0	—	38	0·0	—	53	0·0	—	0·0	—
	AB	84	−1·3	8·6‡	25	12·8	7·5	34	1·0	4·4	1·5	5·0
	B_4	31	−5·5	10·7	6	15·1	11·9	7	2·1	7·7	−0·4	8·7

† Flock 2 fitted mean in terms of the average of the breed crosses concerned.
Flock 3 fitted mean in terms of the Merino sheep.
‡ SE for deviation from Hb type A.
§ No. present in February and March 1972.

face value the results from the first bleeding of flock 3 are inconsistent with this general finding. However, the differences in plasma copper concentration apparently associated with haemoglobin type on that one occasion were statistically non-significant ($0·2>P>0·1$) and the use of a different method of estimating copper might have affected the result. Copper estimations from the same sheep bled a year later showed no differences associated with haemoglobin type. Breed variation in these flocks in the concentration of copper in the plasma as previously reported (*loc. cit.*) was unaffected when haemoglobin type was taken into account (except for the first bleeding of flock 3).

DISCUSSION

The results of the present work show a significant association between haemoglobin type and whole blood copper of sheep in one flock but no significant association between haemoglobin type and copper when estimated in the plasma of sheep in two other flocks.

The inference most readily drawn from the present results is that the difference in copper concentration associated with haemoglobin type resides in the red cells. Alternative explanations are also possible. For example, the associations described may be manifested in some breeds but not in others; but whilst the three flocks studied differed in breeding, there was also an

overlap in breed composition. The possibility also exists that the differences attributable to haemoglobin types may be manifested at some levels of copper but not at others. There is little evidence for this from the present results. Taken at face value, the flock means are not grossly different from each other particularly if some allowance is made for seasonal differences in copper levels—although, as explained earlier, the flock means cannot be strictly compared. Within flocks there is a slight hint that differences showed up more distinctly at the lower average flock levels of copper.

In general, copper concentrations in whole blood and in plasma are thought to be closely correlated (Underwood, 1971). However, some differences in the responses of the copper concentrations of whole blood and of plasma in sheep have been recorded in relation to changing circumstances which include age (McCosker, 1968a), pregnancy and lactation (Butler, 1963; Butler and Barlow, 1963; Howell, Edington and Ewbank, 1968) and nutritional copper status of the flock (Butler and Barlow, 1963; McCosker, 1968b; Suttle, Field and Barlow, 1970).

If direct experimental work confirms that haemoglobin type is associated with copper concentration in red cells, the effect in cells alone is expected to be much larger than in whole blood, since cells occupy, on average, only about a third of the total volume of whole blood. The implications are interesting in terms of the responses of sheep to the nutrient supply of copper. Might cells of different haemoglobin type differ in their susceptibility to copper poisoning whilst at the same time different breeds, for example, show variable susceptibility to copper deficiency?

Highly significant breed differences remained in the concentration of copper in whole blood (and in plasma) after allowance had been made for haemoglobin type, although a part of the breed differences previously reported (Wineer *et al.*, 1969) are now seen to have been attributable to differences in the frequencies of the three haemoglobin types in the different breed groups and as between the pure breeds and the crosses. Haemoglobin type does not, however, seem to have explained the discrepancy noted earlier (Hayter *et al.*, 1973) between flock 3 where crossbred sheep were half-way in their plasma copper levels between those of their parent breeds and flock 1 where crossbred sheep had whole blood copper levels markedly above the mid-parental.

The haemoglobin types of sheep have been shown to affect the concentration of some red cell constituents but only to the extent of 5% or less (Mounib and Evans, 1959; Agar *et al.*, 1972; Hall and Hunter, 1973). The association with copper concentration of whole blood is of a much greater magnitude and requires explanation. In view of the known dependence of haematopoiesis on the presence of copper, more copper may be needed for the formation of the haemoglobin B molecule or for maintaining the integrity of type B and AB cells. However, the causal connexion underlying the association described in this paper may lie between the copper concentration and the haemoglobin genotype rather than the phenotype. This may result from pleiotropic action at this particular locus or from genetic linkage to a gene, or group of genes, with a large effect on copper concentration.

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COPPER LEVELS IN LIVER AND BRAIN OF DEAD LAMBS IN RELATION TO BREED, AGE AT DEATH AND CAUSE OF DEATH

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INTRODUCTION

Breed differences in the concentration of copper in the livers of normal adult sheep were previously reported by Wiener and Field (1969). The same authors (1970) have also given preliminary evidence of breed variation in the concentration of copper in both liver and brain tissue of lambs which died. In general, these findings were in line with a number of studies showing that breeds differed in the concentration of copper both in whole blood and in plasma (e.g. Wiener, Field and Wood, 1969; Wiener and Field, 1971).

The preliminary study of copper levels in liver and brain of dead lambs, based on data from 2 years, also suggested a marked decline in copper concentrations in liver with advancing age at death. This finding, in particular, seemed at variance with the previous report (Cunningham, 1946) that liver levels in normal sheep rise with age. It seemed possible that in the case of the dead lambs, breed and the age differences might have arisen from associations with the causes of death.

This paper presents data from the same flock as that on which the preliminary analysis was based, but the information has been greatly extended to include data from 6 years, and account has been taken of the causes of death and the information on the disease conditions encountered in the course of postmortem examinations on the lambs.

MATERIALS AND METHODS

Animals. The data were derived from an experiment in which the performance of sheep of 3 breeds, the Scottish Blackface, the Cheviot and the Welsh Mountain are being compared with each other and with the crosses among these breeds. For the period covered by the present results (the years 1966 to 1971) each of the breeds and crosses was represented by animals at 4 levels of inbreeding (25·0, 37·5, 50·0 and 59·4 per cent. respectively) resulting from parent-offspring or full sib matings, and by non-inbred lambs produced by crossing unrelated inbred lines. The dams of the

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lambs also included a number of animals of another non-inbred class (F2) present in the flock in an earlier stage of the experiment. All the sheep and their progenitors have been on the farm since 1955 when the females of the foundation flock were purchased as lambs. No males have been introduced to the flock from outside since 1958.

Farm environment and management. The flock is situated at the upland farm of Blythbank in Peeblesshire and is kept out-of-doors all the year round in fields of sown pastures. Supplements of hay and concentrates were offered from midpregnancy, in early February, onward. The flock was run as a single unit except that at lambing the ewes with their lambs were divided into 3 sub-groups according to the week of birth of the lambs and kept in that way until weaning at 15 weeks of age. Thereafter these sub-groups were again amalgamated. During the period of separation the sub-groups were in similar fields and were frequently moved between fields.

Each year in February from 1965 to 1969 inclusive the breeding ewes were given an injection of 50 mg. copper (as copper calcium edetate, "COPRIN", Glaxo Laboratories) to prevent a recurrence of the large outbreak of swayback suffered by the flock in 1964 and because estimations of copper in the plasma of a sample of the flock had suggested low copper levels in each year. In 1970 the plasma levels did not indicate a need for supplementary copper, and none was given. In 1971 copper was given to the ewes as an oral dose of 0·75 g. of copper sulphate in 50 ml. of water.

Post mortem procedure. Out of a total of 658 lambs which died between birth (including still-births) and approximately 8 months of age, a total of 596 were sent for post mortem examination. The 62 dead lambs which were not examined post mortem can be regarded as a random sample of those which died, since failure to send them for examination arose only from difficulties of transport. All specimens were obtained for examination within 24 h. of death. Damage caused by predators together with autolytic changes were therefore reduced to a minimum. Post mortem examination of foetuses and lambs broadly followed the lines described by McFarlane (1965) and Stamp (1967). During the first year, the general examinations were supplemented by more detailed, specialized examinations of specimens covering microbiology, histopathology of the central nervous system and other selected tissues, parasitology and biochemical analysis.

In 1966, biochemical analysis was mainly concerned with liver copper values, but was extended in 1967 and subsequently to include brain copper. Samples were taken for copper determination from most of the lambs dying up to 140 days of age. The small number of lambs with missing copper determinations were spread across all the years and breeds and there was no obvious relationship between failure to send organ samples for analyses and cause of death, except that 5 of the 10 livers classified as "decomposed" had no copper determinations made on them. For purposes of copper determinations, 30 to 50 g. of tissue were supplied from the lateral extremity of the ventral lobe of the liver and 10 to 15 g. from the left occipital pole of the cerebral hemispheres. Selection of these sites was governed by histo-pathological consideration and ease of removal to reduce risks of contamination. From 1967 onward, the specialized examinations, other than the biochemical, were reduced to the minimum thought necessary to assist diagnosis of cause of death.

The information recorded in the course of post mortem examinations was assessed so as to ascribe to each lamb up to 3 factors contributing to its death. In some cases it was considered that one of these represented a clear primary cause with any other factors which may have been recorded making a possible secondary contribution. In many other instances there was no such clear dividing line. For many of the animals the actual cause of death was imprecise or could not be determined. The classification includes categories such as weak lambs or lambs presumed to have died as a result of starvation. In the present study, however, information on causes of death is included primarily to reduce the probability that any associations which might be found between other factors in the flock and copper concentrations, might have arisen through associations between copper levels and causes of death. To this end the causes

of death were regrouped in 2 ways: (1) 15 general categories with each dead lamb placed into 1 category only. There is considerable overlap in the named conditions contributing to each of these categories, but lambs would be placed in the category which most closely described the major symptom, or in a category including more than one symptom if no clear assignment of importance could be made to the different factors contributing to death. The classification so produced was age related such that some conditions, e.g. dystokia, contributed only to early deaths whilst others, such as parasitism, was recorded as a cause of death mainly for lambs dying later in life; a number of other categories, e.g. respiratory diseases, were distributed over all ages. Causes of death classified in this form will be referred to as the "general category". (2) Causes of death were also grouped in a way more specific to the conditions recorded at the time of post mortem examination into the 17 categories shown in Table 4. In this case, each category was recorded according to its presence or absence in the post mortem report. The categories are not therefore mutually exclusive. The results from this exercise will be referred to as derived from the "presence or absence classification".

The results from these 2 methods of classifying causes of death are not strictly comparable except in those cases where a particular factor has been an overriding cause of death and appears as such in both classifications.

Copper estimation. The samples of liver and brain were freeze-dried, milled and 1 g. of the dry matter was wet-ashed (Butler and Newman, 1965). The copper concentration in the ash solution was determined directly by atomic absorption (AA2 Hilger Watts Ltd.).

Statistical procedure. A total of 537 animals was available with complete information on liver copper and 453 with brain copper and these are included in the statistical analysis.

A least squares analysis was used with parameters representing the effects of breed, year of observation, week of birth of the lamb, age of the lamb at death grouped into 7 classes, condition of the liver as recorded at post mortem, the inbreeding of the lamb and separately of the dam, the sex of the lamb, its birth type and type of rearing and the parity of the ewe. The analyses were done with the inclusion of all these factors and for a second time with the inclusion of only the first 5 named since the remainder did not remove a significant amount of variation when fitted into the model. The statistical analyses were repeated with the inclusion of causes of death classified in the 2 ways described in the section on post mortem procedure.

RESULTS

The breed of the lamb, its age at death, the condition of the liver, and the year of observation all contributed significantly to the variation in liver or brain copper levels or both, and these factors along with the causes of death will be discussed in more detail below. Lambs born in different weeks of the lambing season differed significantly in the levels of copper in their livers ($P < 0{\cdot}01$), but there was no consistent trend associated with advancing season. For brain copper there were no significant differences ($P > 0{\cdot}6$) attributable to week of birth. For copper levels in brain, variation associated with inbreeding had a probability of only 0·05 of being due to chance, though there was no obvious trend associated with the 5 levels of inbreeding from 0 to 59 per cent. For variation in liver copper levels there was no suggestion of any association with inbreeding ($P > 0{\cdot}30$). The male–female difference was $10{\cdot}5 \pm 7{\cdot}8$ parts/million for liver copper and $0{\cdot}31 \pm 0{\cdot}27$ parts/million for brain copper. There was no apparent association of copper levels in liver or brain with birth type, type of rearing and parity ($P > 0{\cdot}20$).

Breed

There were considerable differences among the breeds and crosses in the levels of copper in liver and brain dry matter, the variation attributable to breed being highly significant ($P < 0{\cdot}001$). Scottish Blackface lambs had the lowest levels and Welsh Mountain lambs had the highest among the pure breeds. For liver copper the crosses were on average slightly above the mean levels ($P = 0{\cdot}1$) of the pure breeds contributing to each cross. For copper in the brain there was no corresponding overall effect, but for both liver and brain the Blackface-Cheviot crosses had significantly higher copper levels ($P < 0{\cdot}05$) than the mid-parental level. The results are shown in Table 1 and refer only to the statistical analysis in which the cause of death has been classified into general categories. The values are expressed in terms of stillborn lambs. Differences among the breeds were virtually unaffected by the various forms of statistical analysis described, which differed in the number of factors, including causes of death, included alongside breed in the analysis of copper levels.

TABLE 1

THE EFFECT OF BREED ON COPPER CONCENTRATIONS IN LIVER AND BRAIN (PARTS/MILLION OF DRY MATTER) SHOWN AS FITTED VALUES WHEN OTHER FACTORS HELD CONSTANT*

	Liver			*Brain*		
Breed	*No.*	*Fitted value*	*S.E.*†	*No.*	*Fitted value*	*S.E.*†
Scottish Blackface	67	175·3	—	59	9·2	—
Cheviot	74	209·6	14·6	61	10·7	0·52
Welsh Mountain	46	256·0	16·6	41	12·3	0·58
Blackface × Cheviot	157	214·3	13·1	137	11·3	0·46
Blackface × Welsh	110	225·3	13·8	93	10·7	0·49
Cheviot × Welsh	83	243·3	14·8	62	10·6	0·54

* The base class was expressed in terms of stillborn Blackface lambs in 1966 (liver) or 1967 (brain) born on the average lambing date. The base class for the post-mortem classifications was that in which death was ascribed to "general weakness", not associated with disease, and in which the condition of the liver was normal.

† S.E. for deviation from Blackface breed.

Age Trends

Table 2 shows the liver and brain copper levels according to age at death of the lambs. For liver copper there was a clear decline in concentration with increasing age at death and the variation attributable to these differences was highly significant ($P < 0{\cdot}001$). For copper in the brain there were no equivalent differences. The values shown in Table 2 are expressed in terms of the Blackface breed and are those when cause of death has been grouped into the general categories. The trends are not, however, affected to any great extent either by omitting the causes of death altogether or by analysing them in terms of presence or absence. The 3 sets of results are compared in Fig. 1.

Livers and brains of the 85 lambs studied in 1966 were weighed fresh. Only 5 of these lambs were 8 days old or older at the time of death; their average liver

TABLE 2

EFFECT OF AGE AT DEATH ON COPPER CONCENTRATIONS IN LIVER AND BRAIN (PARTS/MILLION OF DRY MATTER) SHOWN AS FITTED DEVIATIONS FROM THE BASE CLASS*

Age at death	*Liver*			*Brain*		
	No.	*Deviation*	*S.E.*†	*No.*	*Deviation*	*S.E.*†
Stillborn	175	—	—	140	—	—
Less than 1 d.	130	−12·6	11·8	109	0·17	0·43
1–2 d.	73	−21·7	16·1	60	0·06	0·57
3–7 d.	57	−52·8	17·9	47	0·04	0·63
8–42 d.	53	−45·3	19·6	49	−0·24	0·67
43–105 d.	26	−92·2	25·2	25	−1·19	0·85
106–140 d.	23	−140·7	26·3	23	0·18	0·88

* See footnote to Table 1.
† S.E. for deviation from stillborn.

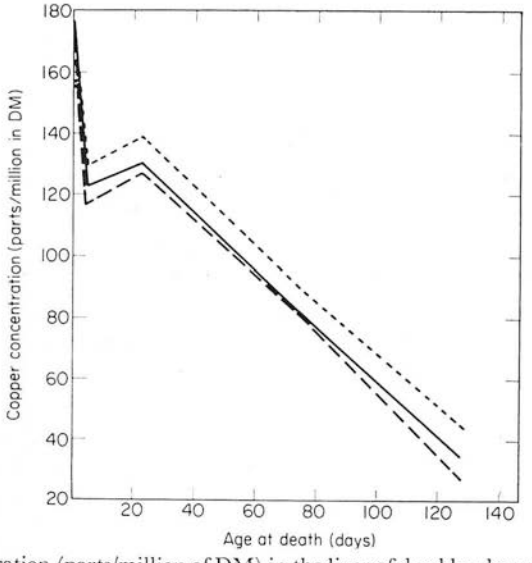

Fig. 1. Copper concentration (parts/million of DM) in the liver of dead lambs according to age at death (fitted values for 7 age groups expressed in terms of the Blackface breed with other factors held constant)*: —, Causes of death classified in general categories (see text); - - -, Causes of death classified by presence or absence of group in the post mortem findings (see text); . . ., Cause of death omitted from analysis.

* Age points are drawn at the mean age for the lambs in each age group.

weight was about double that of the younger lambs and there were no obvious differences in average liver weight among the 4 youngest classes of lamb. Brain weight of the 5 oldest lambs was slightly higher on average than that of the younger lambs.

Liver Condition

Livers were described at the time of post mortem examinations in terms shown in Table 3. Livers showing fatty degeneration, rupture, or haemorrhage

without rupture had higher copper levels than normal livers whilst other liver conditions were associated with lower than normal levels and those with symptoms of hepatitis had the lowest concentrations. The variation attributable to these differences was significant ($P < 0{\cdot}05$). There were no corresponding effects on brain copper levels.

TABLE 3

THE EFFECT OF THE CONDITION OF THE LIVER AS RECORDED AT POST MORTEM EXAMINATION ON COPPER CONCENTRATIONS IN LIVER (PARTS/MILLION OF DRY MATTER) SHOWN AS FITTED DEVIATIONS FROM THE BASE CLASS*

Liver condition	*No.*	*Deviation*	*S.E.*
Normal	355	—	—
Fatty degeneration	37	+35·9	15·2
Internal haemorrages	21	+31·5	19·9
Rupture	51	+28·0	14·4
Congestion	36	−18·4	15.6
Developmental defect	6	−22·4	35·5
Decomposed	10	−33·3	28·1
Hepatitis	20	−40·0	21·8

* See footnote to Table 1.

Cause of Death

Variation in brain copper levels was significantly reduced ($P < 0{\cdot}05$) when the cause of death was included in the analysis in terms of the general categories. For the liver copper the equivalent reduction in variation did not reach statistical significance at this level ($P = 0{\cdot}054$). As explained earlier, however, classification of causes of death in this way was primarily intended to clarify relationships between copper levels and age at death uncorrelated as far as possible with cause of death. The actual copper levels associated with each of these categories is not, however, particularly interesting since the categories contain in most cases more than one factor contributing to death. Table 4 presents the copper levels in relation to cause of death classified by the presence or absence procedure. In respect of any one lamb, the categories listed in this Table are not mutually exclusive. In general, the amount of variation accounted for by taking these causes of death compared with omitting them from the analysis was not statistically significant for either liver or brain copper levels.

Lambs recorded as weak or underdeveloped and lambs with digestive upsets had higher liver copper concentrations than those in which these conditions were absent ($P < 0{\cdot}5$). Very few of the same lambs came into both categories. Neither of the classes were associated with specific diseases and the digestive upsets were of a minor nature. The category of lambs dying at birth for a variety of causes of which delayed birth was the most common had lower copper levels than other lambs also dying at the time of birth for reasons including dystokia, major congenital defects, etc. The class referred to as "swayback" comprised mild cases and in only 1 case was it considered a primary cause of death. Two cases of cobalt pine were also included in this group. The copper level of this group was not significantly different from that of lambs in which this condition was absent. For none of the other individual categories was there any suggestion that copper levels differed for reasons other than chance.

TABLE 4

DIFFERENCES IN LIVER AND BRAIN COPPER LEVELS ACCORDING TO PRESENCE OR ABSENCE OF SOME GROUPS OF CAUSES OF DEATH (PARTS/MILLION OF DRY MATTER)‡

Cause of death group §	*Liver copper*			*Brain copper*		
	No.	*Fitted value*	*S.E.*‖	*No.*	*Fitted value*	*S.E.*‖
Absence of cause		170·6	—		8·5	—
Deviation for presence of :						
Major congenital defect	60	17·4	13·6	42	0·71	0·53
Other congenital defect	30	7·5	17·0	24	−0·23	0·65
Dystokia	121	−8·4	11·4	95	−0·34	0·42
Other deaths at birth	149	−22·2	11·4†	124	−0·07	0·42
Liver rupture	41	−15·1	26·3	28	−0·18	0·98
Respiratory infection	46	3·7	15·4	43	−0·03	0·54
Digestive upset	60	32·8	14·4*	54	0·29	0·51
Digestive disease	69	−13·5	13·3	57	0·03	0·47
Liver disease	15	42·4	30·6	11	−0·39	1·15
Other diseases	44	9·9	16·2	39	−0·48	0·59
Parasitism	18	21·4	27·8	17	−0·26	0·96
Cerebrocortical necrosis	4	12·5	47·0	4	−3·04	1·58†
Suggested swayback and cobalt pine ¶	14	2·9	25·1	13	−0·23	0·97
Weak, underdeveloped	133	24·2	11·0*	127	0·54	0·39
Starvation, exposure	95	5·6	11·8	79	0·61	0·43
Environmental mishap	10	−15·8	28·8	10	0·89	0·97
Unknown	42	−17·4	15·4	25	0·78	0·63

* Significant at $P < 0{\cdot}05$.
† Significant at $P < 0{\cdot}10$.
‡ The base class is as shown in Table 1 except for cause of death which is in respect of the absence of each category.
§ The different groups of causes are not mutually exclusive.
‖ Standard error for the deviation of presence from absence.
¶ Two cases are of cobalt pine.

In the case of brain copper levels only the results for lambs with cerebrocortical necrosis (polio-encephalomalacia) were highly suggestive since the 4 lambs dying from this condition for which brain copper levels were available, all had markedly lower levels when compared with lambs in which this condition was not recorded. Although 10 animals with this condition were recorded, samples of brain were not sent for copper determinations for 6 of them since they were among the animals dying after weaning for which this information was recorded somewhat haphazardly. Attention should be drawn to the virtual absence in these results of significant differences in copper levels when the presence of most of the conditions, including inflammatory diseases and parasitism, were compared with their absence from the postmortem findings.

Year Effects

There were highly significant differences ($P < 0{\cdot}001$) among the years both in respect of liver and brain copper levels. For copper in the liver, concentrations were highest in 1966, approximately 40 parts/million lower over the next 3 years and almost 100 parts/million lower in 1970 and 1971 compared with 1966. For brain copper concentrations where observation started in 1967 the

levels compared with that year were higher in 1968 and 1969 by 1·3 parts/million and lower in 1970 and 1971 by approximately 1 part/million. Among factors which could have contributed to the fluctuations from year to year, only the copper treatment given to the ewes in mid-pregnancy can be specified. The low copper levels in liver and brain in the last 2 years coincide with the absence of a copper injection, although in 1 of these 2 years an oral dose of copper sulphate was given.

Correlations between Liver and Brain Copper Concentrations

After making allowance for the effects of the various factors, such as breed, which affected both liver and brain copper concentrations, the residual correlation equivalent to that within animals was quite low, of the order of 0·38. This suggests that the variation in copper concentration of one organ accounted for less than 15 per cent. of the variation in copper concentration of the other organ.

DISCUSSION

The sheep in the grassland flock from which the present results are derived had equality of nutritional opportunity without, however, any direct control of their intake. There was nothing to indicate that the sheep of different breeds or ages formed separate sub-groups. Under these circumstances the main factors contributing significantly ($P < 0{\cdot}001$) to variation in liver copper concentration were breed, age at death and the year in which the lamb died. For copper in the brain, breed and year were the main factors. The significant factors between them accounted for approximately 40 per cent. of the total variation in liver copper concentration and 30 per cent. of that in brain copper concentration, leaving a considerable amount of variation attributable to unknown or random effects.

Copper concentrations of the breeds ranked in the same order in the present study as for live adult sheep in the same flock in earlier years in respect of their whole blood (Wiener *et al.*, 1969) and their livers (Wiener and Field, 1969). In the earlier study on livers from 68 adults which were killed there was no indication that crossbred sheep deviated significantly or consistently from values half-way between those of the breeds contributing to each cross. The present results show a tendency for the crossbreds to have higher levels than the mid-parental, but short of statistical significance at the 5 per cent. level except for the Blackface–Cheviot cross. Further studies would be needed to determine whether such a difference between the adults and the lambs is attributable to the different ages and condition of the animals involved or is merely due to sampling errors. In neither study of liver copper levels, however, did the crossbred animals have the high copper concentrations relative to the pure breeds recorded for whole blood in the same flock in earlier years (Wiener *et al.*, 1969). For copper levels of the brain there was no indication that crossbreds deviated, at least on average, from the average of the pure breeds.

These considerations are relevant to the inferences that can be drawn about

the mode of inheritance of copper levels. The same ranking of the 3 pure breeds for liver, brain and whole blood copper levels suggests a common basis. The extent to which the crossbreds have different levels relative to the pure breeds for liver, brain and blood points to partial independence of inheritance of their respective copper levels—an inference previously drawn by Wiener and Field (1969) in respect of liver and blood alone.

The fall in liver copper concentrations with advancing age in the present study contrasts with the report of rising levels by Cunningham (1946); but Ryley, Harvey, Watson and Levitt (1961) showed that the livers of lambs at birth had markedly higher concentrations of copper than the livers of their dams. Moreover, normal adult sheep killed in 1966 (Wiener and Field, 1969) from the same flock as the lambs of the present study had lower liver copper levels than the lambs which died after weaning when the comparison is made on a common breed and year basis. In most other species of animal where liver copper has been examined a decline in levels with advancing age has been recorded (see Underwood, 1971) and our results suggest that sheep are likely to follow the same pattern.

The history of swayback on the farm where the present flock was kept (Wiener, 1966) does not rule out the possibility that nutritional copper deficiency contributed to the decline in liver copper levels with advancing age, in spite of the copper dosing of the mothers of the lambs in all but one year. However, even on copper deficient pasture, Cunningham (1946) noted an increase in copper levels of liver dry matter of lambs up to 5 months old, although the levels for "two-tooth wethers" and "aged ewes" on these pastures were lower than this five-month level. Barlow, Purves, Butler and MacIntyre (1960) found that swayback lambs between 6 weeks and 6 months old had liver copper levels of 26 parts/million of DM compared with approximately 6 parts/million for younger swayback lambs—the difference between these groups, however, need not necessarily be attributed to age, but may be explicable in terms of the different sources from which the lambs were derived or in terms of the severity of the swayback. In lambs of the present study, the very limited evidence from fresh liver weights, recorded only in 1966, suggests that total liver copper is likely to have remained relatively unchanged with age as copper concentration fell but liver weights increased.

The inclusion of causes of death in the analysis of the present results has reduced the likelihood that the relationship of copper concentration with age has arisen through correlations with causes of death in general and disease conditions in particular. This is not to say that specific conditions may not affect copper concentrations, but merely to assert that such associations, if they were found to exist, are unlikely to contribute to the present findings. It is not known to what extent the lambs which died were representative of the other lambs alive at these ages, but it would be surprising if they differed greatly, because there was little to associate causes of death with variation in liver copper concentrations. Also in general the results from the dead lambs conform to those from the normal adults previously studied (Wiener and Field, 1969).

The copper concentrations for the different categories of causes of death are interesting mainly in showing that very few associations existed. As reviewed

by Underwood (1971), abnormally high liver copper concentrations are characteristic of a number of diseases of man, but there are no corresponding reports for sheep.

Bremner (1959) has shown depressed liver copper concentrations in dairy calves resulting from experimentally induced parasitic gastro-enteritis. Swayback in sheep has been associated with lower copper concentrations in liver and brain compared to normal by Howell and Davidson (1959) and in the brain, but not the liver, by Mills and Williams (1962). In each case the swayback lambs were from a different source to that of the clinically normal. Shearer, Innes and McDougall (1940), who derived their swayback and normal lambs from the same flock with different treatments, had found little difference in brain or liver copper concentrations between affected and unaffected lambs at the low average levels prevailing particularly for liver. Experimental changes in liver and/or brain copper concentrations have been produced by copper supplementation or by the additions of Mo, SO_4, Fe salts and lead acetate (Butler, Barlow and Smith, 1964; Hemingway, Inglis and Brown, 1964; Suttle and Field, 1968; Abdellatif, 1968). In the present study the lambs in which swayback was diagnosed as only a second or third contributory cause of death (in all cases but one) the copper levels did not differ significantly either in the liver or the brain. The reduced levels of copper in the brain found in the 4 lambs suffering from cerebrocortical necrosis, however, are worthy of special note since even with this small number of cases the probability that the deviation was due to chance was only 0·06.

SUMMARY

Copper concentrations were determined in the dry matter of samples of liver and brain taken from the majority of lambs which had died in a grassland flock of sheep between birth and approximately 5 months of age. For liver copper, the data relate to 537 samples collected over a 6-year-period, and for brain, to 453 samples for the last 5 of these years. The flock comprised the Scottish Blackface, the Cheviot and the Welsh Mountain breeds and the crosses among these breeds. Blackface sheep had the lowest and Welsh the highest concentrations of copper in both liver and brain, the difference being approximately 80 parts/million for liver and 3 parts/million for brain. Among the crossbreds, only the Blackface–Cheviot cross had levels of copper significantly above mid-parental levels.

Age at death was grouped into 7 classes—from lambs that were stillborn to those dying after weaning at 15 weeks of age. Concentrations of copper in the liver declined consistently and markedly with age at death by approximately 135 parts/million over this period. For copper in the brain there was no equivalent change with age.

Both the age and breed differences remained unchanged when account was taken in the statistical analysis of possible correlated effects through associations between cause of death and copper concentration. Factors recorded on a post mortem examination as contributing to death were grouped into 17 causal categories. Only two of these categories, both fairly vague and unrelated to specific diseases, appeared to be significantly associated with a different

level of copper in the liver when the condition was recorded as present than when absent. For brain copper levels, only one of the 17 conditions, cerebrocortical necrosis (polio-encephalomalacia), had a noticeably lower concentration ($-3{\cdot}04 \pm 1{\cdot}58$ parts/million) in the 4 lambs where it was found than in dead lambs without this condition.

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We wish to thank particularly Dr R. M. Barlow who encouraged the detailed post-mortem examinations and participated in 1966, colleagues in the V.I. centre who helped during short absences by one of us (N. S. M. M.) and the staff at Blythbank for the extra work involved in dispatching dead lambs for examination. We are grateful to Dr J. T. Stamp and Dr J. A. Watt for advice and encouragement.

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Seasonal changes, breed differences and repeatability of plasma copper levels of sheep at pasture

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SUMMARY

Plasma copper levels were determined at intervals of 9 weeks over a period of 1 year on 131 female sheep of a grassland flock starting at the age of 5 months in September. The 107 survivors were re-bled 3 years later. There was a steady decline in copper levels from about 100 μg/100 ml plasma in November to about a third of that level at the beginning of the following June. Thereafter there was a partial recovery in level.

Three breeds, Scottish Blackface, Cheviot and Welsh Mountain and their crosses were represented. There were marked differences in plasma copper level among the breeds with cross-breds having levels as high or higher than the corresponding pure breeds. Breed differences in copper levels were already present at 5 months old. Part of the breed differences in copper levels were attributable to differences among the breeds in the frequency of the HbA and HbB alleles.

Correlations were calculated among the plasma copper levels from successive bleedings for individuals within breeds and subclasses. From the time the sheep reached about 9 months old these correlations ranged from 0·4 to 0·9 including bleedings more than 3 years apart in time.

INTRODUCTION

Copper levels both in whole blood and in plasma of adult sheep have been shown to differ among breeds which were maintained together as a single flock (Wiener, Field & Wood, 1969; Wiener & Field, 1971; Hayter, Wiener & Field, 1973). In one of these flocks observations were taken at irregular intervals over a period of more than a year during which there were marked changes in copper levels from summer to winter. It was found that the changes in levels were themselves partly influenced by breed (Wiener, Field & Jolly, 1970). The level observed in early summer, however, may have been affected by a prophylactic copper injection given to the female sheep in January, during early pregnancy. The 'seasonal' changes might also have been influenced to some extent by the effects of pregnancy and the rearing of lambs, although seasonal trends broadly similar to those observed for ewes with lambs were also apparent among barren ewes.

The present study was undertaken to provide information on seasonal changes free from complications of pregnancy and copper injections, but not necessarily free from confounding effects attributable to age changes of the sheep. The experiment was also intended to discover whether breed differences previously observed among adult sheep would be apparent at younger ages and to provide estimates of the repeatability of copper values.

MATERIALS AND METHODS

The 131 female sheep used were born in 1969 in the flock described by Wiener *et al.* (1969) in which breed variation in whole blood copper levels had been observed in an earlier generation. The sheep comprised the Scottish Blackface, Cheviot and Welsh Mountain breeds and the crosses among these breeds and each of these at differing stages of inbreeding (inbreeding coefficient from 0 to 59 %). The different breeds were run as a single flock at grass with a small amount of supplementary feeding of hay from the end of December to the end of

April and concentrates, up to 0·22 kg/sheep/day, from early December to early May. No copper treatments were given to these sheep except in February 1971, after the main cycle of bleedings was completed, when they were given an oral dose of 0·75 g copper sulphate in 50 ml of water. The sheep were not mated until they were about 19 months old. More general aspects of the flock and its management were described by Wiener *et al.* (1969). Blood samples were taken from the sheep every 9 weeks on seven occasions from the age of 5 months onward; a period of 54 weeks. The 107 surviving sheep were re-bled 3 years later. Samples of approximately 20 sheep from this group were also bled in January of 1971, 1972 and 1973. Copper was determined in plasma; the methods are those described by Wiener & Field (1971).

The statistical analyses took the form of fitting a linear model with constants representing the effect of breed, stage of inbreeding of the animal and its dam, and the haemoglobin type (determined by Dr J. G. Hall) for those of the animals which were re-bled 3 years later. Other factors in the original model, but later discarded, included the birth type and type of rearing of the sheep and the parity of its dam. This analysis was carried out separately for every occasion of bleeding. In a second analysis using simultaneously the data from all bleedings, an additional constant was fitted for date of bleeding and for the interaction of breed × date of bleeding, but the latter was subsequently deleted. Residual correlations among the plasma copper levels at the various occasions were calculated after making allowance for the effects of the parameters listed.

RESULTS

Figure 1 shows the general changes in plasma copper levels of the 131 sheep present on each of the first seven occasions and a final point for the 107 survivors bled 3 years later. For the first seven occasions the corresponding values for the 107 survivors alone are almost the same. The estimates from the three sample bleedings are also shown. There was a steady fall in levels from November 1969 to June 1970 followed by a rise. The final value taken 3 years later, in May 1973 soon after most of these females had lambed for the third time, is remarkably similar to the last value recorded in September 1970.

Figure 2 shows the breed deviations from the fitted flock mean calculated separately on each occasion. These deviations show that the Blackface females had, except at the start, the lowest values and the Welsh nearly always the highest among the three pure breeds. Mostly, all three cross-bred types had copper values higher than those of any of the pure breeds, and with one minor exception (the Cheviot–Welsh cross at the seventh bleeding) higher than the average of the corresponding pure breeds. The deviation in copper level of the cross-bred mean from the mean of the corresponding pure breeds was statistically significant ($P < 0{\cdot}05$), or close to this, for the Blackface–Cheviot and Blackface–Welsh crosses but not for the Cheviot–Welsh cross. There was no significant interaction between breed

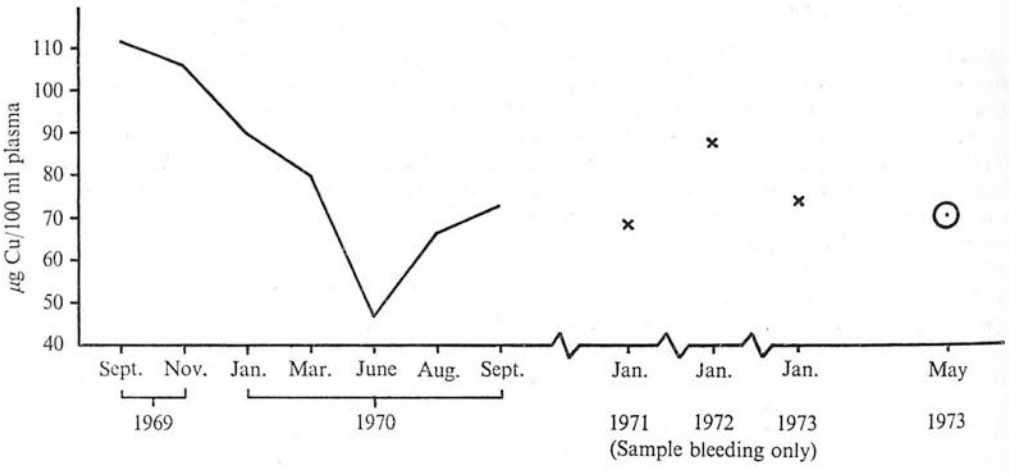

Fig. 1. Plasma copper levels (μg/100 ml) of sheep at different occasions over a 3½-year period (based on 131 sheep for each of the first seven occasions and the 107 survivors (⊙) at the last bleeding. Three intermediate points (×) are based on random samples of approximately 20 of these sheep. Except for the sample bleedings the points represent least squares estimates of seasonal effects for sheep of 'average breed', average inbreeding and average inbreeding of the animal's dam in this flock).

and the occasion of bleeding. The other factors considered, inbreeding of the animal and of its dam, birth type and type of rearing and parity of dam, also had no significant effects on the plasma copper levels. Estimates of breed values in plasma copper levels averaged over the seven bleedings of the first year or the total of eight bleedings are shown in Table 1. The last column in Table 1 shows copper values for breeds after adjusting for the effects of haemoglobin type. These effects are not presented here in detail, but the approximate order of the effect of haemoglobin type in these data was an increase in plasma copper concentration of 19 μg/100 ml for each substitution of the B allele for the A allele. The frequency of the three haemoglobin types (AA, AB, BB) also differed among the breeds and this, apart from some deviations from expectation, is reflected by the differences in gene frequency shown in Table 1. In consequence, breed differences in copper levels can be seen to have been affected by considering them independently of haemoglobin type; the Blackface and Cheviot breeds changed rank as a result of this exercise.

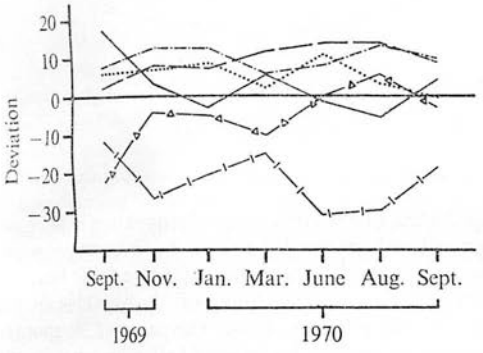

Fig. 2. Plasma copper levels (μg/100 ml) of sheep of three breeds and three crosses shown as deviations from the fitted flock mean separately on each of seven occasions. (The breed values represent least squares estimates of the deviation from the fitted flock mean for sheep of average inbreeding and of average inbreeding of the animal's dam in this flock.) —|—|—, Blackface; △—△, Cheviot; ——, Welsh; – –, Blackface × Cheviot; –·–, Blackface × Welsh; ·····, Cheviot × Welsh.

Table 2 shows residual correlations (equivalent to correlations within sub-classes) among the plasma copper values determined at different times. The residual values ranged from 0·28 to 0·87 and all were statistically significant. In general, correlations involving copper levels at the first and second occasion were on average lower than those involving copper levels at later bleedings although those involving the fourth bleeding (March 1970) were also relatively low. There was also a tendency for correlations between copper levels from successive bleedings to be slightly higher than those separated by an 18- or 27-week gap. However, there was a recovery in the magnitude of the correlation for greater intervals between bleedings. The residual correlation between the copper levels of the adult sheep in May 1973 and that taken in May 3 years earlier was 0·53, and 0·69 with the level in September 1970. Table 2 also shows correlations attributable to the combined effects of breed and haemoglobin type. These were high almost without exception and statistically significant for the most part though based on only 6 degrees of freedom.

DISCUSSION

The results show clearly that on the grassland farm where these sheep were kept, copper levels in blood plasma fell markedly during winter and

Table 1. *Average breed values* (± S.E.) *for plasma copper levels* (μg/100 *ml*) (1) *and* (2) *without adjusting for Hb type and* (3) *after adjusting for* Hb^A *type**

Breed	No. of sheep at each bleeding†	Gene frequency of Hb^A	Hb type: Not fitted (1)	Hb type: Not fitted (2)	Hb type: Fitted (3)
Blackface (B)	19 (13)	0·8	60·0 ± 2·7	57·8 ± 3·1	67·4 ± 3·1
Cheviot (C)	10 (9)	0·1	76·3 ± 3·6	73·8 ± 3·7	60·9 ± 3·7
Welsh (W)	13 (11)	0·7	84·9 ± 3·2	81·2 ± 3·3	88·7 ± 3·2
B × C	34 (30)	0·4	91·3 ± 2·2	92·2 ± 2·3	89·9 ± 2·1
B × W	33 (29)	0·5	91·7 ± 2·3	89·3 ± 2·4	90·1 ± 2·3
C × W	22 (15)	0·5	87·2 ± 2·5	84·5 ± 2·9	84·4 ± 2·7

* Column (1) 131 sheep were bled on seven occasions and columns (2) and (3) 107 of these sheep on eight occasions (for dates see footnote to Table 2). The breed values are based on least squares estimates for the average of all occasions (7 or 8) of bleeding for sheep of average inbreeding and average inbreeding of the animal's dam in this flock. The values in column (3) are, in addition, for copper levels adjusted to the 'average' of the three haemoglobin types.

† Numbers for column (1) and in parentheses for columns (2) and (3).

Table 2. *Residual correlations* (above diagonal) among plasma copper levels determined on* 107 *sheep bled on eight occasions† and correlations attributable to the joint effects of breed and haemoglobin type (below diagonal)*

Occasion† ...	1	2	3	4	5	6	7	8
1		0·42	0·48	0·43	0·40	0·33	0·37	0·38
2	0·73		0·53	0·39	0·28	0·46	0·45	0·35
3	0·77	0·84		0·65	0·42	0·56	0·54	0·50
4	0·81	0·84	0·90		0·42	0·42	0·48	0·47
5	0·72	0·82	0·93	0·95		0·63	0·54	0·53
6	0·68	0·84	0·89	0·96	0·94		0·87	0·66
7	0·77	0·81	0·84	0·98	0·91	0·97		0·61
8	0·72	0·75	0·90	0·95	0·93	0·91	0·92	

* Residual correlations when fitting for the effects of breed, haemoglobin type, inbreeding of animal, inbreeding of dam.

† Occasion of bleeding: 1, 22 September 1969; 2, 24 November 1969; 3, 27 January 1970; 4, 31 March 1970; 5, 2 June 1970; 6, 4 August 1970; 7, 29 September 1970; 8, 15 May 1973.

	Residual (93 D.F.)	Effects (6 D.F.)
Significance: $P < 0{\cdot}05$ for correlations exceeding	0·21	0·71
$P < 0{\cdot}01$	0·27	0·84
$P < 0{\cdot}001$	0·34	0·93

through spring and began to stage a recovery from about the beginning of June, a month or so after grass begins to grow rapidly at this farm. To the extent that plasma copper levels reflect the copper status of the sheep, the decline suggests that either the amount or the availability of copper for the sheep declined during the winter. This decline in copper levels corresponds to a similar decline observed among adult females in the same flock in a previous year (Wiener *et al.* 1969; Wiener *et al.* 1970). From the end of January, however, the sheep in the two studies were treated differently; in particular, the ewes studied earlier had received a prophylactic injection of copper at the end of January.

Butler & Barlow (1963) and Allcroft, Clegg & Uvarov (1959) have shown seasonal changes of copper in the blood of sheep at pasture, particularly on farms, like that of the present experiment, associated with a history of swayback. Their sheep, however, were also pregnant during the period of winter decline in blood copper levels. Evidence for the contribution of pregnancy to the decline is, however, contradictory. Butler & Barlow (1963) attributed part of the observed changes to pregnancy although non-pregnant hoggs also showed a fall in copper levels over the same period. Howell, Edington & Ewbank (1968) noted a drop in plasma copper and caeruloplasmin levels during pregnancy of seven ewes at pasture. Butler (1963) found a substantial fall in copper levels during pregnancy of sheep on a constant diet. Suttle & Field (1968), however, observed no changes in ewes on a copper-supplemented diet. Wiener *et al.* (1969) found that barren ewes had changes in whole blood copper levels generally similar to those of pregnant ewes, though the levels fluctuated a little less.

The fall in copper level of the females in the present experiment from the age of 5 months onward may also be attributable in part to the sheep getting older, since the rise in plasma copper levels of these sheep during their second summer did not bring the levels back to what they had been a year previously. However, seasonal differences cannot be ruled out. Unfortunately, no further observations were taken on these sheep in late summer or early autumn. Suttle, Field & Barlow (1970) recorded a steady fall in plasma copper levels of lambs from about 4 to 11 months of age when given a constant, copper supplemented, diet. Wiener & Field (1971) found that lambs at 3 weeks old had considerably higher copper levels than their mothers but the age difference was confounded with a breed difference, the effect of which was unknown. More recently, Wiener, Hoyte, Field & Macleod (1974) have reported a dramatic fall in liver copper concentrations with advancing age among lambs which had died between birth and 8 months old in the same flock as the sheep on which the present paper is based.

There was marked breed variation in plasma copper levels among the sheep in the present experiment just as there had been in copper levels of whole blood in previous generations in the same flock (Wiener *et al.* 1969). The present results also agree with those recorded earlier in showing that crosses among these breeds to have levels of copper in their blood close to or even above that of the

parent breed with the higher level. It should be emphasized that the cross-bred lambs are born to cross-bred parents. Variation among breeds and crosses in copper levels was significant already at the first bleeding at 5 months old although individual breeds and crosses did not maintain exactly the same relative rank in Cu levels on all occasions. In particular the Cheviot breed average rose and stayed above the Blackface after the first estimate and the Welsh fell below the crosses after that first occasion. On any one occasion, however, only the more extreme of the differences between any two breed values is likely to be statistically significant.

It has been shown previously that the haemoglobin type of sheep is strongly associated with the concentration of copper in whole blood (Wiener, Hall & Hayter, 1973). Since the breeds involved in the present experiment differ in the frequency of their haemoglobin type alleles it seemed appropriate to examine the breed differences in copper levels after making allowance for the possible effects of haemoglobin type. The results on the association found in this experiment between plasma copper concentrations and haemoglobin type will be reported elsewhere (Wiener, Hall, Hayter, Field & Suttle, 1974). It can be seen, however, from the results in Table 1 that the estimates of breed differences in plasma copper levels were affected by this exercise. After taking account of differences in haemoglobin type frequencies two of the breeds, the Cheviot and the Blackface, changed rank. Part of the relatively low level of copper in the plasma of the Blackface breed was attributable to the high frequency of the HbA allele among the sheep of this breed, compared with the low frequency of this allele among the Cheviot.

At any one time sheep in a flock vary quite markedly in plasma copper level, irrespective of breed and haemoglobin type. The present results show that the plasma copper levels of sheep bled at different times are correlated to a considerable degree even over an interval of three years and in the face of large changes in the average level of copper in the flock. The effects of breed and haemoglobin type on plasma copper levels, however, were highly repeatable. Thus in a comparison, as here, of sheep of different breeds and haemoglobin types the total correlation of copper levels of one time with another is higher than the correlation within sub-classes. If extrapolation is warranted from the particular nutritional circumstances of this flock, the prediction of copper levels in blood plasma is likely to be aided by specifying breed and haemoglobin type.

We wish to thank Dr Susan Hayter and Miss Carol Smith for contributing to the statistical analyses of the data and Miss D. Martin for the copper determinations. We are also indebted to Mr Harris, Mr Hughes and their colleagues at Blythbank who willingly undertook the extra work involved by this trial.

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RELATIONSHIPS BETWEEN HAEMOGLOBIN TYPE AND COPPER CONCENTRATIONS IN WHOLE BLOOD AND ITS COMPONENTS IN SHEEP OF DIFFERENT BREEDS

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SUMMARY

Copper concentrations were determined in whole blood, plasma and caeruloplasmin and calculated for red cells and non-caeruloplasmin copper in plasma in 215 female sheep, 9 months old, belonging to the Scottish Blackface, Cheviot and Welsh Mountain breeds of sheep and their crosses. Copper determinations were also made on red cells and plasma, and calculated for whole blood, of a contemporary group of 107 female sheep of the same breeds at the age of 4 years. Further, plasma copper concentrations were determined for these 107 sheep from samples taken on several occasions some years earlier.

Within breed, sheep of type Hb B had significantly higher levels of copper than sheep of type Hb A in whole blood and most of the blood components. The biggest differences were found in plasma and were 19 μg/100 ml for one group and 37 μg/100 ml for the other. Type Hb AB sheep were intermediate in copper level. The differences in plasma copper level associated with Hb type were present and of similar magnitude at different ages, seasons and average flock levels of copper.

After adjustment for the effects of Hb type, breed differences in copper levels were significant for whole blood and all components but much less pronounced for red cells than for plasma.

Copper levels in plasma and red cells were only moderately correlated ($r = 0{\cdot}23$–$0{\cdot}40$).

Combined evidence suggests the existence of a gene with a marked effect on copper level which is linked to the locus for Hb type.

INTRODUCTION

SHEEP of haemoglobin type B (genotype Hb^{BB}) were found, in an earlier study, to have had substantially higher concentrations of copper in whole blood than sheep of haemoglobin type A (Hb^{AA}) whilst sheep of type AB (Hb^{AB}) had copper concentrations approximately half way between those of the haemoglobin type homozygotes (Wiener, Hall and Hayter, 1973). Sheep from two other flocks in which plasma instead of whole blood had been examined were found not to show a corresponding association between

haemoglobin type and copper level. It seemed plausible therefore that the observed differences among sheep of different haemoglobin type were associated with copper in red cells. Alternatively, association of haemoglobin type with copper in one flock but not in others may have been attributable to the fact that different breeds were involved in the three flocks or that there were flock differences associated with environmental or seasonal effects.

The study reported in the present paper was undertaken to test the alternatives by examining the copper concentration of whole blood and a number of its components in two groups of sheep from the flock in which the association of whole-blood copper level and haemoglobin type had been shown. A preliminary report of part of these results was given by Wiener, Hall and Hayter (1974).

MATERIAL AND METHODS

The sheep were drawn from the grassland flock previously described by Wiener, Field and Wood (1969) in which sheep of three breeds, the Scottish Blackface, the Cheviot and the Welsh Mountain, and the crosses among these breeds, are run together and managed alike. In addition, each of the breeds and crosses is represented at four levels of inbreeding as a result of four generations of parent × offspring or full-sib matings. Crosses of inbred lines (non-inbred) were also represented.

Female sheep of two groups were examined:

1. 215 sheep, 9 months old, bled in January 1973.
2. 107 sheep, 4 years old, bled in May 1973.

Haemoglobin type was determined for all sheep and copper concentrations as follows:

Group 1. Determinations were made in whole blood, plasma and caeruloplasmin. Copper in cells was calculated by difference between copper levels in whole blood and in plasma by making allowance for packed cell volume determined for every sample. The difference between total copper in plasma and caeruloplasmin copper (non-caeruloplasmin copper) which was also used as a variable, includes direct-reacting copper.

Group 2. Determinations were made in plasma and in red cells. Copper in whole blood was calculated by the combination of copper levels in plasma and in cells and making appropriate allowance for packed cell volume. In addition, plasma copper concentrations were determined for these sheep from seven successive bleedings taken over a period of a year starting from the age of 5 months (*see* Wiener and Field, 1974).

Copper determinations. Copper in whole blood, plasma and red cells was determined by atomic absorption spectrophotometry. The methods for estimating total copper in plasma were those of Suttle (1974) and in whole blood and red cells by a modification of the method described by Suttle and Field (1968). Red cells and whole blood were digested, using the technique of Thompson and Blanchflower (1971) prior to aspiration. Red cells

were separated from plasma by washing and centrifuging twice in the 30 ml vials used in the digestion process and using ice-cold physiological saline for the wash. The copper of caeruloplasmin was determined by the method of Smith and Wright (1974). Purified sheep caeruloplasmin was used to prepare the standards, and their caeruloplasmin copper concentrations (μg/ml) were estimated by dividing the absorbance (with a 1 cm path length) at 610 nm by 0·024.

Haemoglobin types. These were determined by electrophoresis as described by Wiener, Hall and Hayter (1973). The electrophoretically faster-moving type was called Hb A. Packed cell volume was estimated by microhaematocrit (Hawksley and Sons Ltd, Lancing, Sussex) at 17 000 *g* for 10 min.

TABLE 1

The effect of haemoglobin type on copper concentration (μg/100 ml) in whole blood and its components for two groups of sheep (Group 1, 9 months old; Group 2, 4 years old)

		Copper concentration (μg/100 ml) in									
						Plasma					
						Total (P)		Caeruloplasmin (C)		Difference† (P–C)	
Haemoglobin type	No. of sheep	Whole blood		Red cells†							
		Fitted mean‡	SE of diff.§	Fitted mean	SE of diff.	Fitted mean	SE of diff.	Fitted mean	SE of diff.	Fitted mean	SE of diff.
Group 1											
A	59	47·5	—	50·2	—	47·0	—	31·0	—	16·0	—
AB	97	50·7	3·7	47·1	4·3	53·3	4·6	37·0	4·0	16·3	1·8
B	59	63·7	4·2	61·1	4·8	65·9	5·2	46·9	4·6	18·9	2·0
Signif. of variation		***		**		**		**		NS	
		Whole blood†		Red cells		Total plasma					
Group 2											
A	39	47·1	—	45·0	—	49·1	—	—		—	
AB	28	57·8	8·0	46·7	5·4	63·7	10·7	—		—	
B	40	75·1	7·4	50·3	4·9	86·0	9·9	—		—	
Signif. of variation		**		NS		**					

† Derived as described in Material and Methods section.
‡ Fitted mean in terms of Scottish Blackface sheep and:
For Group 1: sheep which were single born, single reared, non-inbred, born to 2-year-old inbred dams in an average week of lambing.
For Group 2: non-inbred sheep from inbred dams.
§ SE's for deviations from Hb A.

Statistical analyses. These took the form of fitting a linear model with constants representing the effects of haemoglobin type, breed, stage of inbreeding of the animal and of its dam, birth type and type of rearing, parity of dam, and week of birth. For the older sheep (Group 2) some of these factors were dropped from the model since they had no significant effect. The fitted mean for each flock was expressed in terms of sheep of the Blackface breed of Hb type A and other factors as shown on the appropriate Tables.

RESULTS

Hb type. Table 1 shows copper concentrations for whole blood and the components in relation to haemoglobin type. Sheep of type Hb A had lower levels of copper in whole blood and each of the components than those of type Hb B. The difference in whole blood was, however, largely accounted for by the difference in plasma copper concentration. Red cells

were not particularly implicated in haemoglobin-type differences and this is especially apparent from the direct estimates of cell copper made for the adult sheep of Group 2. The difference between the copper levels in plasma and caeruloplasmin showed no significant variation related to haemoglobin type but the trend was in the same direction as for other components. In all cases the copper levels of sheep of Hb AB were slightly closer to the level of type A than type B and for cell copper levels Hb AB sheep were not significantly different from Hb A sheep.

The sheep of Group 2 had also been bled some years earlier at 9-weekly intervals for a period of a year from the age of about 5 months onward. Copper was determined in plasma alone for a study of breed and seasonal

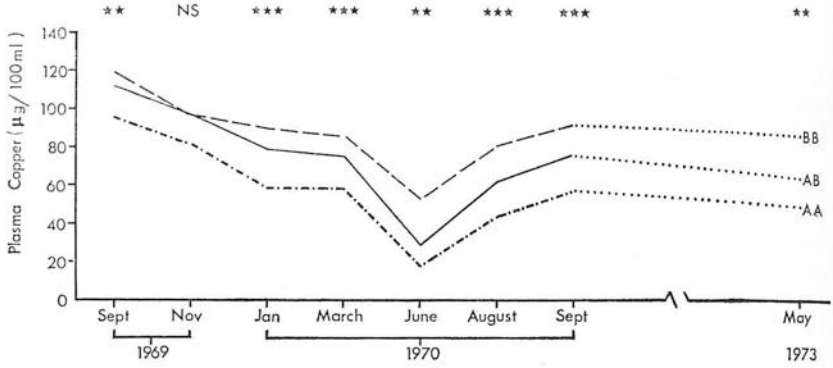

FIG. 1. Plasma copper levels (μg/100 ml) of sheep of three haemoglobin types bled on 8 occasions over a 3½-year period. (The values represent least squares estimates with the fitted mean in terms of non-inbred Scottish Blackface sheep born to inbred dams —see text.)

The significance of variation attributable to Hb type on each occasion is shown by the asterisks along the top of the graph.

variation (Wiener and Field, 1974) but the differences in plasma copper levels on those occasions are shown in Figure 1 related to Hb type. The graph has been extended to include the plasma copper levels for May 1973 (taken from Table 1). Plasma copper levels showed marked changes over the whole period but levels of Hb A sheep were consistently below those of Hb B animals. On the first two occasions Hb AB sheep had copper levels similar to those of Hb B sheep and they remained above a level half-way between Hb A and Hb B until the sheep were about a year old.

Breed. Significant breed differences in copper levels of whole blood and of the various components are shown in Table 2. The breed values are adjusted to the levels of sheep of type Hb A. Since the breeds and crosses varied in the frequency of the three Hb types, breed differences are affected by such an adjustment. In particular, when no adjustment is made for breed differences in Hb type frequency, sheep of the Cheviot breed had higher levels of copper than Blackface. Relative to the pure breeds the copper levels of crossbreds were higher among the old sheep (Group 2) than among the young ones (Group 1). The crossbred 'advantage' was particularly apparent for copper in plasma and either absent (Group 1) or much less pronounced (Group 2) for copper in red cells.

TABLE 2

Copper concentrations in whole blood and its components for different breeds (in two age groups of sheep) after adjustment for breed differences in the frequency of Hb types

Breed	No.	Frequency of Hb types			Copper concentrations (μg/100 ml) in									
									Plasma					
					Whole blood		Red cells†		Total (P)		Caeruloplasmin (C)		Difference† (P–C)	
		AA	AB	BB	Fitted mean‡	SE of diff.§	Fitted mean	SE of diff.	Fitted mean	SE of diff.	Fitted mean	SE of diff.	Fitted mean	SE of diff.
Group 1														
Scottish Blackface (Bf)	36	0·75	0·14	0·11	47·5	—	50·2	—	46·9	—	31·0	—	16·0	—
Cheviot (Ch)	11	0·00	0·18	0·82	53·4	7·6	58·4	8·7	51·1	9·4	36·4	8·3	14·6	3·7
Welsh Mountain (W)	26	0·31	0·46	0·23	68·9	5·3	51·5	6·1	77·3	6·6	58·3	5·8	19·0	2·6
Bf × Ch	59	0·05	0·58	0·37	61·5	4·8	40·9	5·6	71·0	6·0	50·4	5·3	20·6	2·4
Bf × W	47	0·26	0·55	0·19	56·8	4·9	48·4	5·6	61·0	6·1	45·9	5·3	15·1	2·4
Ch × W	36	0·25	0·50	0·25	58·4	5·1	57·1	5·9	59·6	6·4	44·2	5·6	15·4	2·5
Signif. of variation						**		*		***		***		*
Group 2					Whole blood†		Red cells		Total plasma					
Scottish Blackface (Bf)	13	0·70	0·15	0·15	47·1	—	45·0	—	49·1	—	—		—	
Cheviot (Ch)	9	0·00	0·22	0·78	37·3	14·5	53·1	9·7	32·1	19·4	—		—	
Welsh Mountain (W)	11	0·64	0·18	0·18	52·3	12·1	47·9	8·0	55·3	16·1	—		—	
Bf × Ch	30	0·27	0·23	0·50	68·9	10·5	51·9	7·0	77·4	14·0	—		—	
Bf × W	29	0·31	0·41	0·28	69·7	11·0	56·6	7·3	77·2	14·6	—		—	
Ch × W	15	0·40	0·20	0·40	59·4	11·8	56·2	7·8	63·2	15·7	—		—	
Signif. of variation						*		NS		*				

† Derived as described in Material and Methods section.
‡ The fitted mean for sheep of Hb type A as further described in footnote to Table 1.
§ SE for differences from Scottish Blackface.

Correlations. Residual correlations (equivalent to correlations within sub-classes) among the copper levels in whole blood and its components are shown in Table 3. Most consideration should be given to the correlations among the independently determined parameters, i.e. whole blood, plasma and caeruloplasmin in sheep of Group 1; plasma and red cells in Group 2. It can be seen, however, that the correlations involving 'calculated' values for red cell copper (Group 1) and whole blood copper (Group 2) are of similar magnitude to those involving the independent determinations. Not unexpectedly, copper levels in whole blood were highly correlated with those in plasma (both total and caeruloplasmin copper) and strongly with that in red cells. Perhaps of greater interest are the much less close relationships between copper levels in separate components of blood in particular between plasma and red cells ($r = 0{\cdot}23$ or $0{\cdot}40$).

TABLE 3

Residual correlations† among copper levels in whole blood and its components in two groups of sheep (Group 1, 9 months old, figures in Roman; Group 2, 4 years old, figures in italics)

	Copper concentration in:				
			Plasma		
	Whole blood	Red cells	Total (P)	Caeruloplasmin (C)	Difference (P–C)
Copper concentration in:					
Whole blood		0·56	0·93‡	0·86‡	0·44
Red cells	*0·56*		0·23	0·22	0·08
Plasma					
Total (P)	*0·98*	*0·40*‡		0·92‡	0·49
Caeruloplasmin (C)	—	—	—		0·11

† After fitting for the effects of breed, haemoglobin type and other factors detailed in footnote to Table 1. (d.f. for correlations: Group 1, 194; Group 2, 93)

‡ Based on independent copper determination of each parameter.

Other factors. Most of the other factors for which adjustment was made in the calculation of the effects of breed and haemoglobin type had only small or non-significant effects on copper levels.

DISCUSSION

The flock of sheep from which the animals in the present study were drawn had been closed since 1958 when the last purchased rams were introduced. In the circumstances the present results are not independent of earlier findings in the same flock, but confirm that a part of the variation in copper levels of blood recorded among earlier generations of sheep in this flock has a genetic basis. This was observed as variation among breeds (Wiener and Field, 1966; Wiener *et al.*, 1969) and haemoglobin types (Wiener *et al.*, 1973). In the present paper, results on copper levels in red cells, caeruloplasmin and the non-caeruloplasmin copper in plasma are presented for the first time for this flock.

As shown by the residual correlations there appears to be no strong association between the concentrations of copper in red cells and in plasma —at least for the two occasions recorded in this study. Accordingly, variation in copper levels of whole blood is likely to be more closely related to the variation in plasma than to that in red cells, since plasma is the major component. None the less, since genetic variation is assumed to represent only a part, albeit a significant part, of the total variation in the copper concentration of whole blood there is no *a priori* way of deciding to which of the components of whole blood to attribute genetic variation. It is of interest therefore to note that breed variation in copper levels is much less marked for red cells than for plasma (or caeruloplasmin) and hence a large part of the breed variation in whole blood is attributable to differences in plasma. Similarly the association between copper levels in whole blood and the haemoglobin type of the sheep are mainly associated with differences in plasma. This must now be considered alongside the absence of such an association in two other flocks studied by Wiener *et al.* (1973).

The differences in plasma copper levels related to haemoglobin type were seen to be present (in Figure 1 for sheep of Group 2) at different times of year, at ages from 5 months to 4 years and over a wide range of average copper levels for the flock. This shows that variable environmental factors did not override the differences associated with Hb type. It does not seem very likely therefore that the absence of a corresponding association in the two other flocks referred to is attributable to differences in environment.

The combined evidence of the present study and the earlier one (Wiener *et al.*, 1973) suggests that the differences in blood copper levels associated with Hb type are unlikely to result from pleiotropic action of the Hb alleles, or from a physiologically different demand for copper by red cells of different Hb types. In the latter case one would expect the copper level to vary (with Hb type) in red cells rather than in plasma. And in both these circumstances the association with Hb type would have been expected to be universal, that is, present in all sheep and all flocks, apart from any modifications due to environmental circumstances or interactions with other genes.

The evidence is, however, consistent with the hypothesis that there may be a single gene which exerts a large effect on copper levels. Further, that the locus for this gene is linked to the Hb locus. In the flock under discussion the presumed 'gene' for 'high' copper appears to have become more often associated with the Hb *B* allele, or that for 'low' copper with the Hb *A* allele, than the reverse. That this association is not complete is then shown by the fact that the difference in copper level between Hb types is much greater in some breed groups than in others. This, however, could also depend on the frequency of the presumed high and low copper gene present in the different breed groups. Similarly, the failure to find an association between Hb type and plasma copper levels in the two other flocks referred to (Wiener *et al.*, 1973) would then be attributed either to an absence of a directional association or to an absence of variation in the copper alleles present in those populations. The latter possibility, an absence of variation in copper alleles, seems unlikely since in both these flocks there were large and highly significant differences in plasma copper levels among the nine breeds involved (Wiener and Field, 1971; Hayter, Wiener and Field, 1973). Nonetheless, it may now be of some interest to recall that on the first of three occasions when one of the other flocks described by Wiener *et al.*

(1973) was bled, Hb B and Hb AB sheep had distinctly higher plasma copper levels than did sheep of type Hb A—although these differences were not statistically significant and were completely absent at two subsequent bleedings of the same animals.

The fact that the present flock had been closed for many years, was started from a relatively small foundation (approximately 40 females and 6 males per pure breed) and intense inbreeding had been practised, may have provided particular conditions for fixing or maintaining the association between Hb type and the presumed 'copper type' predominantly in one direction. However, it must also be considered that the direction of the association may not be a chance one. Natural selection may have favoured this particular combination for although it has not been found, as yet, within other breeds with any certainty, there is an indication, from limited data, that across breeds there is an association between blood copper level and frequency of Hb type A in the same direction as in the present study (Wiener *et al.*, 1973).

It has not yet been possible to test the 'copper gene' hypothesis with parentage data because until very recently rams in this flock were not tested for copper level. A breeding experiment has, however, been initiated for this purpose.

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Selection for plasma copper concentrations within haemoglobin type in sheep

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The observation that plasma copper concentrations were strongly associated with haemoglobin type in sheep in one flock but not in other flocks (Wiener, Hall and Hayter, 1973; Wiener et al., 1974) led to the hypothesis that there exists a gene with a major effect on plasma copper levels and that the locus of this gene may be partly linked to the haemoglobin-type locus. To test this hypothesis an experiment was designed in collaboration with Dr. S. Hayter (A.B.R.O.) in which rams were selected within haemoglobin type A and within haemoglobin type B for high and for low plasma copper levels. The selected rams were then mated to an unselected group of ewes. The effects of the selection of the rams were studied by examining the plasma copper levels of the progeny. The concentrations were determined by Dr. A.C. Field (Moredun Research Institute). Drs. Hayter and Field will be co-authors of any publication of this work.

Material and Methods

The experiment was conducted with grazing sheep on the farm of Blythbank in Peeblesshire. The flock and its general management were described by Wiener, Field and Wood (1969). The rams used were from the Scottish Blackface-Welsh Mountain cross, which had been inter-bred for several generations. This 'breed' was chosen because the Hb A and Hb B alleles occurred in approximately equal frequencies and

because there was a particularly strong association between haemoglobin type and plasma copper concentration in this 'breed'.

There were eighty-nine rams available from which sires could be selected on the basis of plasma copper levels. Blood samples were taken on August 31, 1973. Haemoglobin typing by Dr. J.G. Hall showed that 27 of them were of type Hb A and 29 of type Hb B. The remainder were type Hb AB. Ram lambs and older rams were included in the group, some being inbred and others non-inbred. Statistical analysis showed a large age difference in plasma copper concentrations; the levels of young rams (about 5 months old) being on average almost three times as high as those of the older rams. Non-inbred rams had slightly higher levels than inbred ones. Selection was therefore based on copper levels adjusted to the levels of young, non-inbred rams by means of fitting constants by least squares. The two rams with the highest and the two rams with the lowest plasma copper concentrations of haemoglobin type A and separately the two rams with the highest and the two rams with the lowest plasma copper concentration of haemoglobin type B were then selected for service. The 'lowest' ram of type Hb B was subsequently found to be incapable of producing semen and the ram with the next lowest plasma copper concentration had to be used instead. Rams of type Hb AB were not used in the experiment. Table 1 shows the plasma copper concentrations (on August 31, 1973) of the eight rams used for mating which commenced in November 1973.

Table 1

Plasma copper concentrations (µg Cu/100 ml plasma) of selected rams used in matings adjusted to the level of young, non-inbred rams

		HAEMOGLOBIN TYPE	
		A	B
Copper group			
High	ram 1	193	239
	2	187	235
Low	ram 1	75	125
	2	97	146

The selected rams were mated to 105 Blackface, Welsh or Blackface-Welsh females from the grassland flock described in the earlier study (Wiener et al., 1974). The females, which were 19-month old, were allocated so that each ram was mated to an appropriately equal proportion of females of Hb types A, AB and B and to avoid inbreeding. Apart from this, allocation was random, no account being taken of the plasma copper levels of the ewes.

The lambs, which were born in April and May 1974, were kept at grass with their dams until 15 weeks of age when they were weaned. They were then kept at grass without supplementary feeding until 29 weeks of age (approx.) when they were sold for slaughter. Up to weaning, blood samples were taken from lambs at 3, 6, 9, 12 and 15 weeks old (± $3\frac{1}{2}$ days). Thereafter, blood samples were taken on three occasions when the average age of the lambs was 18, 24 and 29 weeks. On the last three occasions the age range of the lambs sampled was close to ± 3 weeks. Blood samples were obtained from the dams three

weeks after the birth of their lambs. Plasma copper concentrations were determined on these samples.

Statistical analysis took the form of fitting a linear model to obtain estimates of the effects of the selection group of the sire (high or low copper), the haemoglobin type of sire, breed, and haemoglobin type of dam, and birth type, type of rearing (single or twin) and week of birth of lamb. Plasma copper level of dam was also included in the model but excluded for the calculation of correlations with lambs' plasma copper level. Effects on the lamb's copper levels of selection for 'high' or 'low' copper levels of sire were thus statistically adjusted for the effects of haemoglobin type of parents (i.e. equivalent of being within haemoglobin type) and effects of sire's haemoglobin type were similarly adjusted for the effects of selection for 'high' or 'low' copper level.

A total of 124 lambs were born of which 13 died (all before weaning). There was no indication that the proportion dying differed with haemoglobin type of sire or copper level of sire. A further 7 lambs each had at least one missing copper determination. The results are based therefore on the 104 lambs with complete sets of data to the 29 weeks of age when the experiment had to be terminated.

Results and Discussion

The most important result relates to the effects of the rams' plasma copper level (high or low) and haemoglobin type (A or B) on the plasma copper levels of their progeny. These are shown in Figure 1 as fitted values.

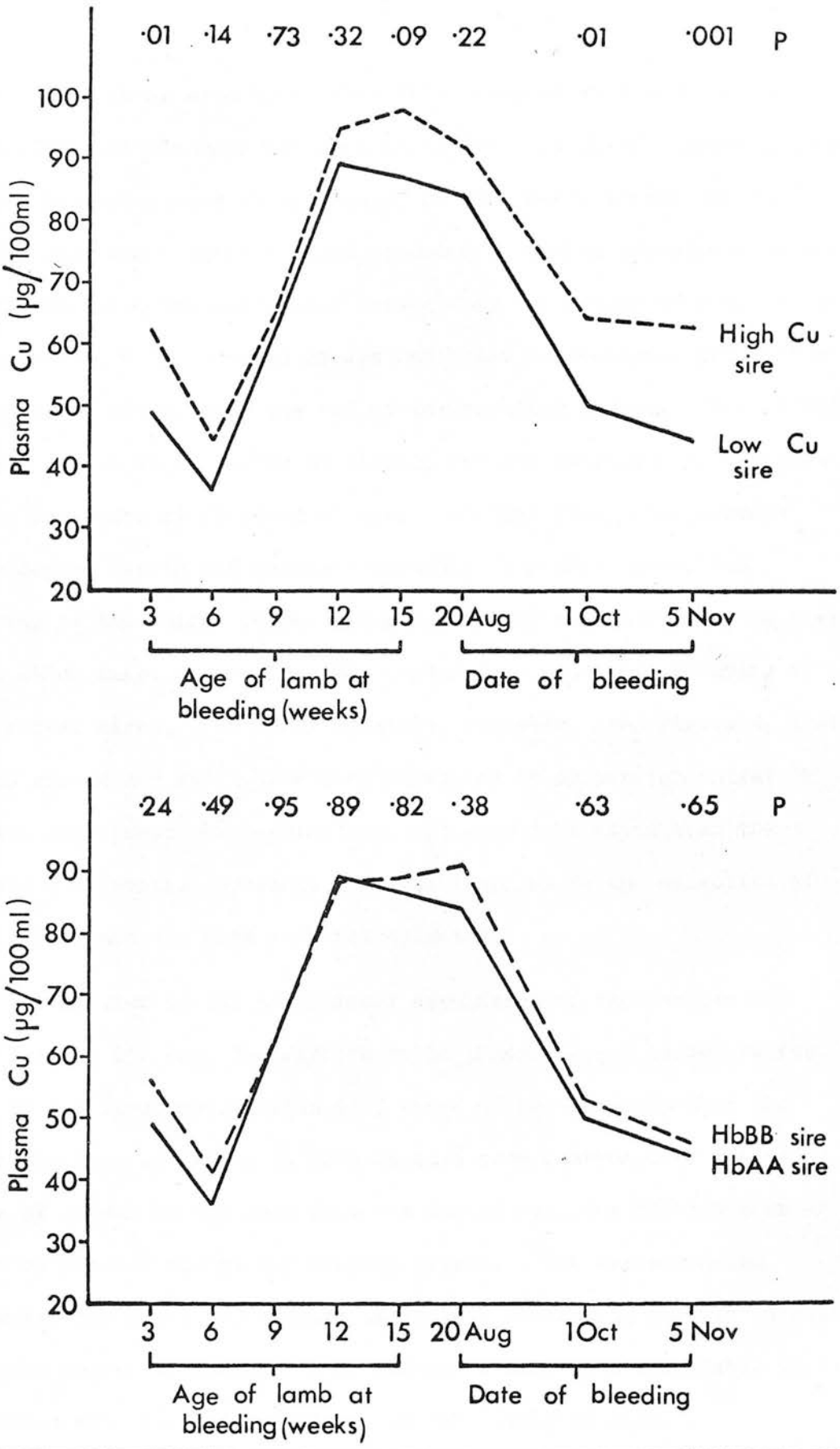

Fig. 1. Plasma copper concentrations of lambs at 8 ages (fitted values, see text).

a) upper figure: the offspring of sires selected within haemoglobin type for high or for low plasma copper concentration

b) lower figure: the offspring of rams of type HbA and HbB.

Above each graph is shown the probability (P) that a difference of the magnitude observed at each age could be due to chance alone.

It can be seen that, when first sampled at 3 weeks of age, the offspring of the rams selected as having high plasma copper concentrations themselves had significantly higher plasma copper concentrations than the progeny of rams selected as having low plasma copper concentrations. The difference between the two groups of progeny had disappeared at 6 and 9 weeks of age and began to re-appear from around the age of 12 weeks, near the end of the suckling period. The difference had become 18 µg Cu/100 ml plasma, and statistically high significant, for lambs at 29 weeks of age. At that time, when average plasma copper levels had declined markedly from their peak, the offspring of the 'high' copper sires had copper concentrations in their plasma which were, on average, 40% higher than those of offspring of 'low' copper sires. It seems possible, moreover, from Figure 1, that the two groups may still have been diverging in copper concentration when the experiment was terminated. It should be noted that the observed differences represent only the response to the selection of the sires, since the dams were not selected.

In view of the nutritional dependence of the newborn and young lamb on its dam, the difference in plasma copper concentration found at the first observation at 3 weeks of age suggests that the lamb's genotype is likely to have exerted some control over the early uptake of copper by the lamb from its dam or over the distribution of copper as between plasma and storage organs. The corresponding difference for older lambs could indicate a continuing genetic influence on copper uptake or distribution, but could also be attributable to a difference established pre-natally or very early in life.

The absence of a difference in plasma copper concentration between the offspring of the two types of ram at 6 and 9 weeks (and a non-significant difference for some time thereafter) may be due to chance variation in the sire effect, but other factors should be considered such as the likelihood of changes in the supply of copper to the lamb (for changes in copper content of ewe's milk, see Ashton and Yousef, 1966; Beck, 1941) and changes in the rate of absorption of copper by the lamb during this period (Suttle, 1975).

The residual correlation (equivalent to a correlation within sub-classes) between dam's plasma copper level 3 weeks after parturition and her lamb's plasma copper level at successive bleedings declined from a value of 0.6 for lambs at 3 and 6 weeks old to 0.4 at 9 weeks, 0.2 at 12 weeks and 0.3 at 15 weeks when the lambs were weaned. Interpretation of this trend as a decline in maternal influence on the plasma copper level of the lamb must, however, be treated with caution because of confounding with the increasing time interval between the single bleeding of the dams and the successive bleedings of their lambs.

The lower part of Figure 1 shows that the difference in plasma copper concentration between offspring of Hb A and Hb B rams was negligible.

The observed effect of selecting rams for high or for low plasma copper concentration on the plasma copper levels of their lambs clearly raises a number of questions concerned with the mechanisms whereby the differences arose or were maintained and which the present experiment was not designed to answer. However, in respect of its

main purpose, the experiment has provided results consistent with the hypothesis that the association previously observed in the same flock between haemoglobin type and plasma copper level is not due to an effect of the gene controlling haemoglobin type, and is due effectively to a 'copper gene'.

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Breed differences in repletion of plasma copper concentrations following depletion

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The evidence for genetic variation in the concentrations of copper in blood, liver and brain of sheep (see, for example, Wiener and Field, 1969; Wiener, Field and Wood, 1969; Wiener and Field, 1971; Hayter, Wiener and Field, 1973; Wiener, Hayter, Field and Macleod, 1974; Wiener, Hall, Hayter, Field and Suttle, 1974) poses the question of how these differences arise. One possibility is that genetic differences exist in the rate of absorption of dietary copper. An experiment was undertaken therefore to compare the rate of repletion of plasma copper concentrations following depletion in several breeds. One of the breeds used for the purpose had been drawn to our attention (Garden, personal communication) as being particularly susceptible to copper poisoning on 'normal' diets and hence possibly 'extreme' in its ability to absorb dietary copper. The breed concerned, Orkney sheep from the island of North Ronaldsay, subsists predominantly on a diet of seaweed in its native habitat.

The experiment was conducted in collaboration with Dr. N.F. Suttle (Moredun Research Institute) who was responsible for the diets used and for testing the plasma copper concentrations of the sheep. Dr. Suttle will be a co-author of any publication of this work.

Material and Methods

The following breeds, crossbreds and numbers of lambs were available for the main part of the experiment.

North Ronaldsay	(NR)	9
Welsh Mountain	(W)	4
Scottish Blackface	(B)	5
W x NR		7
B x NR		6

The crossbred lambs had the North Ronaldsay breed as their sire (several rams of each breed were involved).

Lambs were taken from their dams within 24 hr. of birth and reared artificially on a cold milk substitute containing less than 1 ppm Cu. They were given milk substitute alone for 3 weeks and were then allowed access to a pelleted, semi-purified diet containing less than 1.5 ppm Cu. The liquid feed was progressively withdrawn after the lambs were 5 weeks old and stopped at 6 weeks.

Blood samples were first taken from the lambs at approximately one week of age and every 2 weeks thereafter. Plasma copper concentrations averaged 124 µg/100 ml at first. The aim was to deplete each animal to a level of plasma copper of around 30 µg/100 ml plasma before repletion by means of feeding a diet containing approximately 3.5 ppm Cu for 5 weeks.

The time taken for plasma copper concentrations to decline to the required level varied among lambs and apparently among the breeds involved. Interpretation of these differences is difficult,

however, since the dams of the lambs were not treated exactly alike and because this could be related to the time taken to deplete. Since repletion was intended to start at the same time for all lambs, it was necessary to keep the most rapidly depleted lambs on a 'standby' diet containing 2.5 ppm Cu until the plasma copper concentration of the others had been reduced to the required level.

Feeding was ad libitum. During the repletion phase, lambs were individually penned and their food intake recorded. Liveweights of the lambs were also recorded and blood samples taken once a week for determinations of copper concentrations. The lambs were on average 29 weeks old at the start of the repletion phase.

Results and Discussion

Figure 1 shows the change in plasma copper concentrations during the 5-week repletion period. The most rapid rise occurred in the North Ronaldsay lambs, whilst there was virtually no change in the plasma copper concentrations of the Blackface lambs; lambs of the Welsh Mountain breed showed a slight rise and, interestingly, the copper levels of the crossbred lambs rose during the 5 week period to almost the level of their paternal breed (the North Ronaldsay), but at a slower rate.

Although the breeds differed markedly in liveweight and food intake (the North Ronaldsay being only a little over half the weight of the Blackface, and the others intermediate) these did not explain to any significant extent the differences in the rate of repletion of plasma copper concentrations shown in Figure 1. It is of interest to

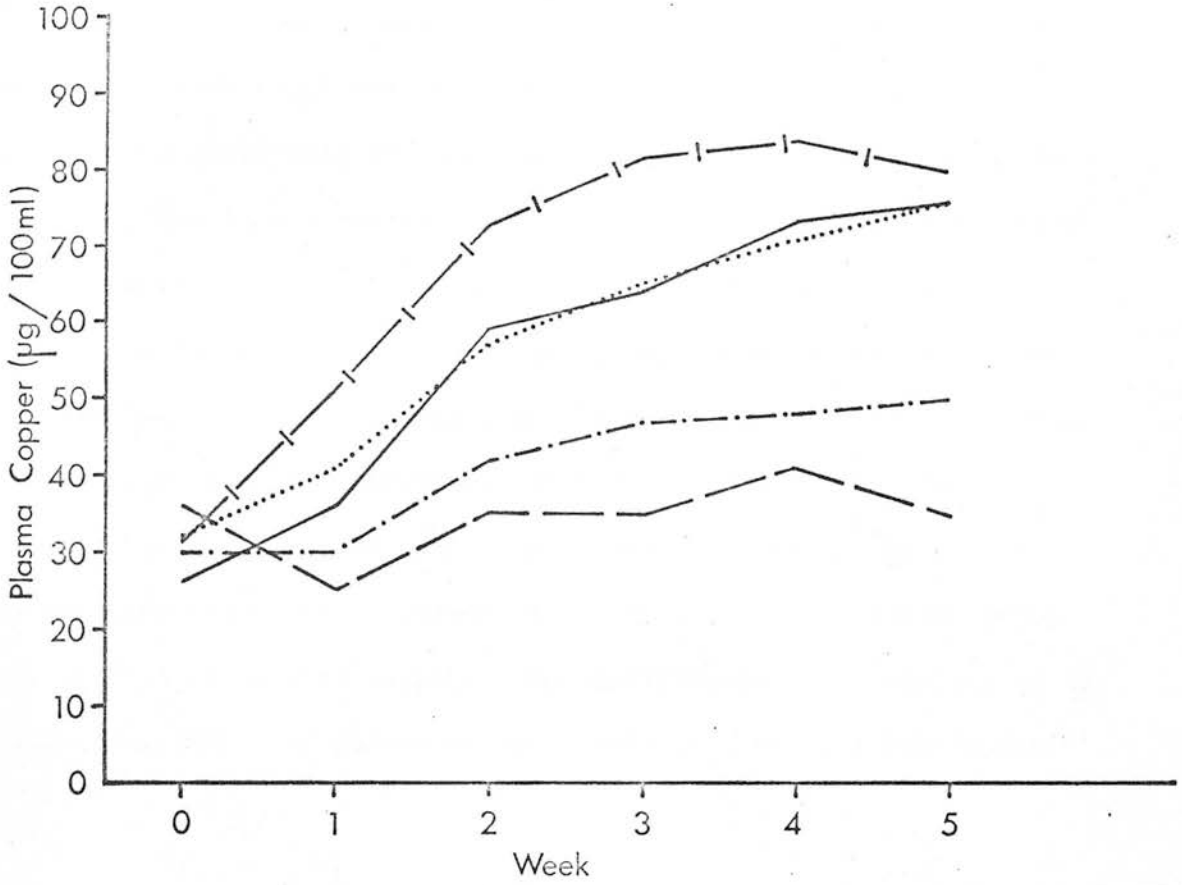

Fig 1. Changes in plasma copper levels of 5 breed groups of sheep over a 5 week period when given a diet containing approximately 3.5 ppm. of copper following a period of copper depletion.

—|——|— NORTH RONALDSAY (9 animals)

—·—·—·— WELSH (4 animals)

— — — — BLACKFACE (5 animals)

———— WELSH x NORTH RONALDSAY (7 animals)

..... BLACKFACE x NORTH RONALDSAY (6 animals)

note, however, that the most rapid repletion occurred in the North Ronaldsay breed which was included in this trial because of its alleged susceptibility to copper poisoning. Conversely the absence of a response to the repletion diet occurred in the Blackface breed which was included in this trial because of its relative susceptibility to the copper deficiency syndrome, swayback, (Wiener, 1966) and because of its low plasma copper concentration relative to other breeds under grazing conditions (Wiener, Field and Wood, 1969). Susceptibility to copper poisoning on the one hand and to copper deficiency on the other, suggest that there are differences in the utilization of dietary copper. The differences here observed in the rate of repletion of plasma copper levels support this hypothesis.

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ON THE USE OF MUZZLE PRINTS IN THE DIAGNOSIS OF MONOZYGOSITY OF CATTLE TWINS

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(With One Text-figure)

In search for a test whereby cattle twins could be positively identified as of one- or two-egg origin, muzzle pattern has been tried as a criterion by many workers. Muzzle prints of cattle were thought to be analogous to fingerprints of humans, but widely varying amounts of importance in twin diagnosis have been attached to them by different workers. Muzzle prints from a large number of one-egg and two-egg cattle twins were available for study in Edinburgh, and investigations with these described here are thought to shed new light on this subject. Also, a different technique of muzzle printing from that used by other workers has been employed, and is thought to lend weight to our observations.

A wide range of views, supported by arguments which will be considered later, has been held on the use of muzzle prints in twin diagnosis. Early work set out to establish their individuality for each animal. The earliest quoted by Salomon (1930) and Hering (1931) was that of Boehme (1909). Later work by Petersen (1922), Littwitz (1924) (quoted by various authors, original not seen), Salomon (1930), Hering (1931), Habu (1935) (only abstract seen), and Hirsch, Graham & Dracy (1952) established the following points with regard to muzzle prints:

(1) No two patterns from different individuals have ever been seen to be identical by any one of the workers in this field (the biggest single group of prints seems to be that of Habu, with over 5000).

(2) The pattern remains the same throughout the life of the animal; although the pattern may become more distinct with advancing age, it does not alter.

The authors quoted above, and those referred to later, have employed some form of inking process to obtain their prints of the muzzle pattern. Methods are described in detail by Salomon (1930), Hering (1931) and Nadai (1949).

Classification has depended on the presence (or absence) and length of a central groove dividing the pattern into two halves. Further subdivision has taken account of the direction of radiating grooves, and how far the ridges thus formed are broken into cells by subsidiary grooves. The number of cells in each ridge, and the regularity of the pattern, have been examined. Littwitz decided on four main types of pattern, Salomon on seven, Hering on three, Habu on four, and Hirsch *et al.* on four principal patterns before proceeding to subdivision.

Hering attempted to determine the inheritance of the muzzle pattern by using progeny groups of two bulls and employing twenty twin pairs. He failed to reconcile his classification with any simple genetic theory—assuming control by two or three genes. He recognized three 'phenotypes' designated R, V, and U. For one set of comparisons between the progeny of one bull (type R) and their dams, it can be seen that the differences in the totals of the three pattern types in dams and offspring are highly significant ($P = < 0{\cdot}001$). Table 1 shows these data.

Table 1. *Classification of muzzle pattern of dams and their progeny by a bull phenotypically 'R'*

(After Hering, 1931.)

Sire's type	Dam's type	No.	No. of progeny according to type		
			R	V	U
R	R	69	60	7	2
R	V	42	17	24	1
R	U	42	23	14	5
		153	100	45	8

$\chi^2 = 154$; D.F. $= 2$; $P < 0{\cdot}001$.

In the matings shown in Table 1 (type R bull on three types of cow) there are significantly more 'R' types among the offspring than among their dams, and it is concluded from this that muzzle pattern is inherited. Nothing is known, however, about the repeatability of the classification. Moreover, later in the same paper, Hering complicated the picture by representing his phenotypes, not only by the three shown above, but also by combinations of them (R/V : V/U : U/R). This suggests a continuous distribution.

Attempts to use muzzle pattern in the diagnosis of monozygosity of cattle twins were generally based on the assumption of a high heritability for this character. Kronacher (1932), Schmidt & Kliesch (1938), Haak (1943), Bonnier in an early account

(1946), and Nadai (1949) have all attached great importance to the muzzle pattern. Hancock (1949), on the other hand, sets little store by it as a criterion of monozygosity because of the existence of only three or four readily distinguishable types.

Other workers who have examined muzzle patterns of cattle twins with a view to using them in twin diagnosis, include Sanders (1935), Kronacher & Sanders (1936), Dry (1942), and Dracy, Graham & Hirsch (1953). Keller & Niedoba (1937) studied the patterns on fifteen pairs of double monsters and classed ten pairs as 'very similar', 'similar', or 'similar and mirror imaged', and one pair as 'slightly similar'; the other four pairs were intermediate.

More recently, Johansson & Venge (1951) have dealt with muzzle pattern as a criterion in twin diagnosis by comparing similarity on a 1–5 scale within two-egg twin pairs and within 'random' pairs (i.e. unrelated animals of similar age). The repeatability of scoring was 0·596 for twins and 0·455 for random pairs when the relationship between the individuals of each pair was not known to the scorers. The average scores varied with scorers, and observations from 2·07 to 2·42 for twin pairs and from 1·25 to 1·83 for random pairs (1 = unlike; 5 = very alike). The greater similarity of muzzle pattern within twin pairs than within random pairs is an indication of the influence of heredity—although it could, at least theoretically, be due in part to the common prenatal maternal environment of the twins.

Nadai (1949) has tried to supplement subjective evaluation of muzzle pattern by a quantitative measure. In this case, the number of ridges cut by the circumference of a circle inscribed in a triangle whose three corners were the base of the central groove and points on the margins of the nostrils at the narrowest part of the print (between the nostrils). He noted within pairs the difference in the number of ridges (papillarlinien) cut and claimed for fifteen pairs of one-egg twins an average difference of 0·3 and for a similar number of two-egg twins an average difference of 3·5. It is doubtful, however, whether it is legitimate to draw conclusions about the diagnostic value of these measurements. The one-egg twins used by Nadai had been kept at Wiad, Sweden, and muzzle pattern had certainly been a criterion in their original diagnosis (Bonnier, 1946; Bonnier & Hansson, 1948). Further, two-egg twin data were collected by Nadai from Swiss cattle, and do not therefore apply to the same population.

METHODS

The technique of muzzle printing used by us for the past 4 years is to take a plaster cast of the animal's nose. The method was suggested by Mr D. W. Wotherspoon of the Royal Scottish Museum after the more conventional ink methods had failed to give satisfaction.

The procedure of making the cast is as follows. An impression of the nose is taken in putty which has been kneaded soft but not sticky. A mass of this putty about 3 to 4 cm. thick and slightly larger than the animal's nose is placed on a clock glass and applied with even pressure against the animal's nose—which has first been wiped with a dry cloth. Contact need not be longer than 1 or 2 sec., and is usually so brief that the animal does not object. It is desirable to open the beast's mouth slightly by inserting a thumb. The mould obtained is filled with plaster of Paris mixed with water to the consistency of thick cream. It has been found expedient to use a mixture of plaster of Paris and quick-setting artificial stone mixture (about 3 to 1) in order to increase the hardness of the finished cast. The setting time of the mixture is very little longer than that of plaster of Paris alone. After 5–10 min. the cast is sufficiently hard to take out of the mould, but it should be allowed to dry off for some time before extensive handling. The cast should be labelled and the procedure adopted here was to press a paper label bearing identification on to the upper surface of the cast while still soft and in the mould.

Plaster casts are thought to have the following advantages over ink prints:

(1) Contact with the animal's nose is shorter.

(2) Small amounts of moisture on the nose do not disturb.

(3) Grooves and ridges on the cast are not likely to be the result of faulty technique as occasionally happens with ink prints when over- or under-inking may affect the portrait obtained.

(4) The cast being three-dimensional accurately potrays size relationships of cells on different parts of the nose.

RESULTS

Quantitative measurements were tried both on the casts and on photographs of the casts. Factors considered were sizes of individual cells, numbers of ridges cut by 'fixed' lines (after Nadai), number of cells per unit area, number of pores per cell, and so on. In every case, the technical difficulties of measurement could not be overcome to give a reasonable repeatability. The main difficulty was to find fixed points from which to proceed.

It was decided, accordingly, to try to score subjectively the similarity of muzzle patterns of one-egg and of two-egg twins purchased by the Animal Breeding Research Organization. The procedure seemed justified because in field diagnosis of twins, muzzle pattern was not included in the reasons for rejecting pairs as not one-egg, and because the reports on twins purchased as one-egg

show that muzzle pattern was not a significant criterion in diagnosis. The twins whose casts were studied can be presumed to be virtually unselected for muzzle pattern.

Scoring. Similarity of muzzle pattern for pairs of twins was scored on a scale rising from 1 (maximum observed dissimilarity) to 5 (minimum observed dissimilarity). Two aspects of the pattern considered were the general type and details. Concordance in details was considered important only when members of a pair showed fair agreement in general type of pattern.

A scoring trial was conducted (November 1952) on the following lines: casts from 129 pairs of one-egg twins (MZ's) and 60 pairs of two-egg twins (DZ's) were available. From each of these two groups 40 pairs were picked at random. Two observers (1 and 2), both familiar with muzzle patterns did the scoring to the plan illustrated below:

		Observer 1	Observer 2
Scoring (i)	Morning 1	Table A	Table B
	Morning 2	Table B	Table A
	Morning 3	No scoring	
Scoring (ii)	Morning 4	Table A	Table B
	Morning 5	Table B	Table A

After the first scoring (i) the pairs of casts were rearranged on the tables.

No results were known to the observers until the completion of the whole trial. The observers did not know whether they were scoring MZ's or DZ's only that 20 pairs of each kind were on each table (see above). The purpose of these precautions was to minimize, as far as possible, effects of time of day (lighting), the state of mind of the observer, and the possibility of memorizing particular pairs of casts.

The scores averaged for each observer and the intra-class correlations between scorings are shown in Table 2, along with the results of a second scoring trial done on a larger number of pairs 6 months later (see below).

The differences between the mean scores of MZ's and DZ's are highly significant ($P = < 0{\cdot}001$) for each observer, and so are the correlations between scores. In no case in the scoring trial of November 1952 did the repeat score differ by more than one point from the first. In an analysis of the data, summarized in Table 3, the difference between scorings was not significant. Differences between MZ's and DZ's, observers, tables and casts, were all highly significant ($P = < 0{\cdot}001$). First-order interactions were not significant when tested against the error term, and have been added together. Higher order interactions, also not significant, have been included in the error term. If the variances are tested against that of 'casts' (variance arising between pairs), the difference between MZ's and DZ's remains highly significant ($P = < 0{\cdot}001$), that between observers is still significant at a level between 1 and 5%, and the difference between tables becomes non-significant.

Table 3. *Analysis of variance of muzzle pattern scoring for cattle twins (November 1952)*

Source	D.F.	Variance	Variance ratio
MZ − DZ	1	22·578	148·20***
Observers	1	8·778	57·62***
Tables	1	2·628	17·25***
Scorings	1	0·003	0·02
Interactions	6	0·128	0·84
Casts	76	1·446	9·49***
Error	233	0·152	—

*** $P = < 0{\cdot}001$.

That mean scores of observers differ significantly is not disturbing since the trial was not intended to allocate definite scores to individual pairs, but merely to ascertain whether more than one observer would find that the mean scores of MZ and DZ pairs were significantly different. As Table 3 shows, the largest single item in the total variance stems from the difference between MZ's and DZ's. Differences between Tables A and B must have been due to chance.

A feature of the first trial was considerable overlap in the score distributions of one-egg and of two-egg twins except at the extremes of the scale. Since this bears directly on the use of muzzle pattern in twin diagnosis, casts from 110 pairs of MZ's and 60 pairs of DZ's were scored twice by observer 2, 6 months after the original trial. Average scores and correlation between scorings are shown in the last line of Table 2 and agree closely with the results of the previous trial.

Table 2. *Average scores (scale 1–5), for muzzle pattern of twins and intra-class correlation of scorings*

Date of scoring trial	Observer	MZ pairs Mean	MZ pairs S.D.†	DZ pairs Mean	DZ pairs S.D.†	Intra-class correlations between scorings (i) and (ii)
November 1952	Observer 1	3·23	±0·66	2·74	±0·69	0·496***
	Observer 2	2·94	±0·68	2·36	±0·72	0·604***
May 1953	Observer 2	3·00	±0·70	2·43	±0·75	0·613***

† Of single score. *** $P = < 0{\cdot}001$.

The two scorings in the second trial, when averaged, were distributed for each group of twins as shown in Fig. 1. It can be seen that no MZ's were scored below 2 and no DZ's above 3·5. The range of scores both for MZ's and for DZ's and of the overlap of scores was the same in the previous scoring trial. The skewness of the DZ score distribution seen in Fig. 1 was not noted in the previous trial and is due to six pairs with average score 2·5 then, being scored 3·0 on the later occasion. For the seventy-five pairs which were scored on both occasions the correlation between the averages of the two scorings each time is 0·690 ($P = < 0{\cdot}001$).

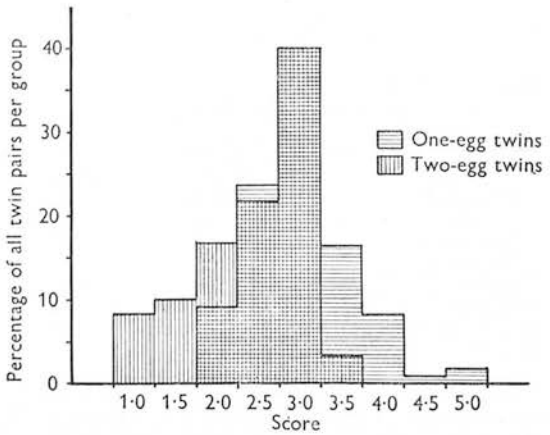

Fig. 1. Percentage distribution of average scores for muzzle pattern (110 pairs of one-egg and 60 pairs of two-egg twins).

Details of muzzle patterns. Having found as a result of the scoring trials a general similarity of pattern within pairs, an attempt was made to find out whether this general resemblance could be related to similarities in details of the patterns of 313 casts. For each, four characteristics were described as follows:

(1) Central groove: (*a*) present and long; (*b*) rudimentary in length or absent.

(2) Cell length in central area of the cast: (*a*) at least twice as long as wide; (*b*) less than twice as long as wide, or a mixture of long and short cells.

(3) Cell margins: (*a*) relatively wavy; (*b*) relatively straight.

(4) The two halves of the pattern each side of a central vertical division: (*a*) symmetrical; (*b*) asymmetrical.

Each cast was described twice with a day's interval between observations. The description and identification of the cast was recorded by an assistant and not referred to by the observer until after the trial. On the standard set by the observer, nearly all patterns were described as symmetrical, so that character (4) was not further analysed. The two observations on each trait were pooled; characters could then be described as corresponding to (*a*) or to (*b*) in the classification, or could be 'doubtful' because the repeat observation was different from the first. The doubtful cases could be due either to the borderline nature of the traits or to observational errors.

Of the 313 casts, 264 were members of twin pairs; for these the recorded observations were paired with the result shown in Table 4. The frequency in each category expected on the basis of random pairing is also shown. Assuming some genetic control of the traits involved, the results are in the direction expected, i.e. concordance in twin pairs of both kinds is greater than would be expected in random pairing. The deviation from expectation is significant at the 5 % level for central groove (MZ and DZ) and for MZ cell length (χ^2 4·45, 5·01 and 4·33 respectively, 1 D.F.). MZ pairs showed slightly greater concordance for cell length and cell margins than DZ pairs but not significantly. If expectation in random pairing is calculated from frequencies in all 313 casts instead of the 264 members of twin pairs in Table 4, deviations from expectation are significant only for MZ cell length (χ^2 16·49, $P = < 0{\cdot}001$) and approach the 5 % significance level for DZ cell length (χ^2 3·43).

DISCUSSION

Since this and earlier studies show that one-egg twins resemble each other in muzzle pattern more than two-egg twins, and all twins more than random pairs, heredity must influence this trait. Discussion

Table 4. *Within-pair comparisons for characters of muzzle pattern*

		Number of pairs			
		MZ		DZ	
Character	Members of the pair	Observed	Expected in random pairing	Observed	Expected in random pairing
Central groove	Same	70	60·0	29	22·5
	Different	26	36·0	7	13·5
Cell length	Same	61	50·8	21	19·1
	Different	35	45·2	15	16·9
Cell margins	Same	56	48·9	19	18·3
	Different	40	47·1	17	17·7

of these findings is confined, however, to their usefulness in twin diagnosis as the material is unsuitable for assessing mode of inheritance or heritabilities.

For diagnosis, subjective judgements on muzzle patterns may be treated in two ways. In one, the individual animal and in the other the twin pair is the unit judged. Into the first category come descriptions of cell length, cell margins, and central groove, or Hering's pattern 'types' (R, V, U). On the criteria presented earlier, concordance or discordance within twin pairs does not lead to a positive diagnosis. This is because dizygous twins are not sufficiently less similar than monozygous and because a considerable proportion of pairs are alike purely by chance arising from the small number of classes within each criterion and the high frequency of one of the classes in each trait.

Into the second category come the quantitative measure of similarity of muzzle patterns proposed by Nadai, and the similarity scoring of Johansson & Venge and of the present study. The overlap noted in score distributions of one- and two-egg twins makes this method useful in diagnosis only as confirmatory evidence at the extremes of the similarity scale. Thus, prints showing very slight discordance in pattern are unlikely to be from two-egg twins, whilst those quite dissimilar both in general pattern and in details are most improbably of one-egg origin. In practice, the latter consideration is the more useful as it is the more easily recognized and because a number of two-egg twins show such dissimilarity, whereas great likeness is unusual even with one-egg twins.

SUMMARY

1. Past work on muzzle patterns of individuals and of twins is reviewed.

2. A technique of obtaining muzzle prints by making plaster casts is described.

3. Using casts, muzzle patterns from one-egg and two-egg twin pairs were scored for similarity on a 1–5 scale. Patterns of one-egg twins were significantly more similar than those of two-egg twins, and the largest part of the total variance was due to the difference between these two groups. The score distributions for monozygous and dizygous twins did not completely overlap, indicating that muzzle pattern is inherited. However, the extent of overlap observed confines the usefulness of muzzle pattern in twin diagnosis to confirmatory evidence at the extremes of the similarity scale.

4. Parts of the muzzle pattern (central groove, cell length, and cell margins) were judged on an arbitrary scale. Two-egg twins were not found sufficiently less similar than one-egg twins for the characters to be useful in diagnosis. Twins were more alike than random pairs, but significantly so only for central groove and MZ cell length.

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OBSERVATIONS ON MANDIBULAR PROGNATHISM

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The interest which has recently developed in mouth abnormalities in bulls submitted for licensing invites some consideration of the genetical aspects. " Mouth abnormalities" is much too vague a term for this purpose. Defects of teeth and tongue have been reported as well as of the jaws and skull generally, so it is necessary to say at the outset that the discussion will be limited to defects involving the jaws. The term " undershot jaw " has been avoided as it has been used in two opposed senses—for the mandible which is too short relative to the upper jaw (Hancock, 1949), as well as for the mandible which is too long (Nordby, 1935 ; Miller & West, 1953). Part of this paper is devoted to a general review of the literature on the subject of variation in jaw length, and part to a study of this variation in samples of British cattle.

REVIEW OF LITERATURE

Nordby *et al.* (1945) have pointed out that it would be erroneous to assume that unequal jaw lengths arise only from variation in the length of the mandible. Mandibular prognathism could arise from a shortening of the upper jaw as well as from a lengthening of the lower. Indeed both, theoretically at least, could be abnormal for a given breed and result in either correct or incorrect dental occlusion. What is normal for one breed of sheep may, according to Hitchin (1948), be abnormal for another. Although perhaps not obviously true of sheep, the sentiment certainly applies to pigs and dogs, some breeds of which are characteristically prognathic, while others have relatively light short mandibles. Evidence of a considerable degree of developmental independence of upper and lower jaws is not far to seek. Long-nosed dogs, such as show collies and greyhounds, are prone to short lower jaws (Miller & West, 1953). Crosses between long-nosed and short-nosed dogs carried out by Stockard (1941) showed that the growth of upper and lower jaws was often imperfectly co-ordinated. The implication is that some at least of the genes affecting the length of the lower jaw act independently of those controlling the length of the upper jaw.

In cattle, single genes can bring about inequality. Darwin (1882) described the niata cattle of South America which probably had been bred homozygous for a gene achieving such a marked reduction in the nasal and premaxillary bones that the incisor teeth jutted outwards and upwards in ludicrous fashion. To save the animals in time of drought, they had to be hand-fed because they were ill-adapted to browsing on trees and shrubs which sufficed for normal cattle.

Becker & Arnold (1949) describe a family of grade Jersey cattle in which occurred individuals, apparently homozygous for a recessive gene, with short broad heads, shortened nasal bones and prominent prognathic lower jaws showing an excessive upward curvature like the skull of a niata animal illustrated by Vasey (1857) and reminiscent of the head of a " bulldog " Dexter calf. Surrarer (1943) refers to three similar cases in Jerseys. Various degrees of inherited achondroplasia involving skull proportions have been reported and reviewed by Gilmore (1949). Agnathia has been reported by Heizer & Hervey (1937) and Annett (1939), and listed by Lerner (1944) as characters A14 and A19. Ranstead (1946) thinks both are due to the same recessive gene. Ljutikov (quoted by Lerner, 1944) reported the occurrence of short-legged calves with lower jaws too short to permit of grazing, and Ely *et al.* (1939) described foetal calves without lower jaws.

More recently, a form of dwarfism in Hereford cattle has been described by Johnson *et al.* (1950) which may be relevant to the problem of prognathism in British beef breeds. Their data suggested that the dwarfs were homozygous for a recessive gene, and that heterozygotes, although apparently normal, might be favoured for breeding purposes because they come nearer to the ideal conformation than do homozygous normals. Gregory *et al.* (1951) confirm the hypothesis of a recessive gene, and assert that homozygous dwarfs as calves have body proportions rather like those of a mature normal beast. They often breathe heavily as if the respiratory passage were obstructed, their heads are short and wide (brachycephalic), and nearly all show a protruding lower jaw with incisor teeth that miss the dental pad by $1\frac{1}{2}$ to $3\frac{1}{2}$ cm. A bulging forehead and a misshapen mandible are characteristic (Gregory *et al.*, 1951). All these features recall hereditary cretinism, and the dwarfs are claimed in fact to be deficient in thyrotrophic pituitary hormone (Carroll *et al.*, 1951), although Johnson *et al.* (1950) stated that the thyroid gland was active. In later papers, Gregory and his co-workers (1952, 1953) show that heterozygotes may be distinguished by their head profiles and state that, owing to preference by breeders for them, the dwarf problem has reached serious economic proportions. Unfortunately, no mention is made of the lower jaw in heterozygotes. No evidence of the occurrence of such dwarfs in British beef cattle appears to have been published, but it is clearly of considerable interest to know whether or not they do occur.

The most extensive and careful study on jaw inequalities seems to have been carried out by Nordby *et al.* (1945) on sheep. They were able to show that sheep deficient in length of lower jaw had longer skulls and shorter mandibles than normal sheep. Only minor degrees of inequality were compensated for by the angle of emergence of the incisor teeth so that the teeth continued to meet the dental pad. If the incisor teeth did not meet the pad, some factor other than pressure by it determined the angle. At the age of weaning affected lambs were no more variable in weight than normals, but significantly lighter. Some animals changed in grading for jaw length with age, but the change was not always for the better and the authors make no generalisations. Genetically, the short lower jaw condition did not turn out to be simple. Several pairs of genes were probably involved, and some at least were dominant in action. Supporting evidence that heredity can account for short lower jaws in sheep is given by Young & Purser (1954) who found four seriously affected weaned lambs in a flock of 140 composed of seven breeds and crosses. All four were Scotch Blackfaces from one of two contributing stocks, and all died.

Both anatomically and genetically, the normal matching of jaw lengths is complicated. Failure to achieve it could theoretically arise from (*a*) foetal and post-natal malnutrition (cf. Warkany & Nelson, 1941 ; Franklin, 1950) ; (*b*) developmental accident ; (*c*) one gene of recognisable effect acting predominantly on one or other jaw ; or (*d*) two or more non-allelic genes causing developmental disharmony. It is not necessary to suppose in all cases that the causative genes act specifically on jaw length. They may induce a lack of stability in development which makes the skull bones in general, and

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579. A STUDY OF VARIATION IN TWIN CATTLE

IV. EMERGENCE OF PERMANENT INCISOR TEETH

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Permanent incisor teeth of cattle are commonly used for estimating age, but there is little information about either the magnitude or sources of normal variation in age at eruption. An opportunity to study this variation was presented by the uniformity trial of twins and half-sibs discussed in earlier papers in this series and described in the first (4). The data also furnish a useful test of the possibility suggested by King & Donald (7) that the variation shown within pairs of one-egg twins might not be a correct measure of environmental effects within pairs of half-sisters treated uniformly like the twins. If increasing departure from genetic identity attracts increasing contributions of variation not due to the additive effects of genes, the point is of considerable practical and theoretical importance. The purpose of this paper, therefore, is to examine this point as well as some of the sources of the variation in age at eruption of incisor teeth shown by liberally fed cattle.

Youatt (19) gave 2, 3, 4 and 5 years as the approximate ages at which to expect the 1st, 2nd, 3rd and 4th pairs of permanent incisors. In a most detailed account, Simonds (12) stated that age at eruption is influenced by breeds and 'other causes'. He divided cattle into early and late groups on the basis of differences in this character. According to Miller & Robertson (9) ages at eruption are influenced by 'domestication, methods of management and the nature of food, and what applies to the more highly specialized improved breeds does not apply to the commonly bred cattle, and what applies to these latter does not apply to ranch cattle'. Zorn (20) is also of the opinion that breed and feeding, as well as individuality, account for variation in age at eruption of incisors in German cattle. Brown (3), however, in a booklet on dentition, written originally at the beginning of this century but recently revised, questions the truth of the assumption that breeding and feeding affect the emergence of teeth. He states that over more than half a century, during which the management of cattle altered appreciably, he noted no marked changes. Average ages at eruption are quoted by many other authors, but the source and extent of their observations are not always apparent.

The regulations of the Smithfield Club Show (14) in respect of permanent incisor teeth are: 'Cattle having their central permanent incisors cut will be considered as exceeding one year and six months. Cattle having their central permanent incisors fully up will be considered as exceeding one year and nine months. Cattle having their second pair of permanent incisors fully up will be considered as exceeding two years and three months. Cattle having their third pair of permanent incisors cut will be considered as exceeding two years and eight months. Cattle having their fourth pair (corner) permanent incisors fully up and their anterior molars showing signs of wear will be considered as exceeding three years.' Most authors report slightly greater average ages. The Smithfield ages might

be chosen therefore either to make allowance for the relatively early eruption of teeth claimed for high quality beef cattle, or to establish a workable definition of age.

Franklin (5), and workers quoted by him, have shown that food deficient in calcium will adversely affect both incisor and molar development in sheep. Tooth size in mice was particularly sensitive to the kind of food their dams were given during pregnancy and lactation (11). Thyroidectomized sheep showed delayed eruption of teeth, though the order of eruption was not changed (8, 16). In man a number of conditions are known to delay eruption, but very few which speed its onset (15). It may be concluded that certain gross dietary or physiological deficiencies will cause deviations from normal eruption and growth of teeth, but that not much is known of the sensitivity of developing teeth to the less conspicuous influences of heredity and husbandry.

MATERIAL AND METHODS

For the present study, fifteen pairs of one-egg twins (MZ), fourteen pairs of two-egg twins (DZ), and thirteen pairs of half-sibs (HZ) were available. All the animals, for the care of which Mr D. Anderson was responsible, were on the same high plane of nutrition throughout their life and belonged to a variety of breed types and crosses. Fortnightly observations, limited to permanent incisors, were made from the age of 15 months. Five stages of eruption were recognized and recorded as 1 (just through the gum), 2, 3, 4 and 5 (fully up). Complete emergence was, like other stages in eruption, judged subjectively. Owing to gradual culling of the animals after their first lactation, the number of observations available for analysis diminished with each successive pair of teeth.

It should be added that what is described here as the 4th pair of permanent incisors is regarded by dental anatomists (17) as a pair of mandibular canines. The use of the term 'incisor' for this pair is based on the nomenclature of Sisson & Grossman (13).

RESULTS

Age at eruption of permanent incisors

Age at eruption is highly variable—more so than might be supposed from the practical use to which it is put. First incisor teeth may emerge as much as 5 months before or after the due date (about 2 years) and later teeth vary even more. The result is that some animals have, for instance, their 3rd pair at an earlier age than that at which others have their second pair. As shown in Table 1, which records the age at eruption for each tooth individually, the earliest of the 1st incisors in this material appeared soon after 18 months of age and the last of the 4th incisors at 4 years and 10 weeks. The distributions of ages at eruption show a slight positive skewness for all pairs of teeth, which increases from 1st to 2nd to 3rd incisors; that for the 3rd incisors is statistically significant ($P = 0{\cdot}02$). Skewness for the 4th incisor is somewhat less than for the 3rd on one test for skewness and somewhat greater on another.

The increasing range of ages noted in Table 1 is associated with an increasing variance in age at eruption (Table 2) such that the coefficient of variability remains constant at about 8%.

The average interval between eruptions of successive pairs was roughly 6 months, though possibly the last pair was a little overdue on this reckoning. Means and variances

Table 1. *Distribution of age at eruption of permanent incisor teeth*

Age at eruption (weeks)	1st	2nd	3rd	4th
79–82	1	—	—	—
83–86	4	—	—	—
87–90	15	—	—	—
91–94	27	—	—	—
95–98	26	—	—	—
99–102*	32	—	—	—
103–106	31	—	—	—
107–110	14	—	—	—
111–114	12	11	—	—
115–118	4	17	1	—
119–122	2	24	—	—
123–126	—	24	—	—
127–130*	—	23	4	—
131–134	—	24	6	—
135–138	—	11	7	—
139–142	—	7	15	—
143–146	—	6	13	—
147–150	—	1	25	—
151–154*	—	—	21	2
155–158	—	—	6	3
159–162	—	—	8	9
163–166	—	—	6	2
167–170	—	—	5	11
171–174	—	—	4	13
175–178	—	—	4	9
179–182*	—	—	1	8
183–186	—	—	1	8
187–190	—	—	1	7
191–194	—	—	—	9
195–198	—	—	—	6
199–202	—	—	—	2
203–206	—	—	—	4
207–210	—	—	—	2
211–214	—	—	—	—
215–218	—	—	—	1
Totals	168	148	128	96

* Mean value included in range.

Table 2. *Age at eruption of pairs of permanent incisors in cattle twins and half-sibs*

Incisor pair	No. of animals	Mean age at eruption (weeks)	Mean square of age at eruption	Mean interval between eruptions (weeks)
1st	84	100·4	58·2	—
2nd	74	127·1	67·8	26·7
3rd	64	151·2	153·8	24·1
4th	48	180·0	199·4	28·8

in Table 2 apply approximately to the three contributing groups, and to the forty-eight animals from which data are complete.

Although ages at eruption have been averaged for each pair of teeth in Table 2, there is some variation between left and right teeth which requires notice. In 30% of the 270 pairs of teeth studied the left and right tooth of each pair erupted during the same fortnight; the left tooth appeared first by one or more observation periods in another 30%; and in 40% of all pairs the right tooth erupted before the left. Furthermore, when the right erupted before the left member of a pair, the time interval between the two appearances was found to be a little greater than in pairs of which the left came first. The net effect, averaged over all animals and pairs of teeth, was that right teeth appeared nearly 10 days

before left teeth—a difference which is statistically highly significant. The interval, however, between eruption and full size of each tooth was about 2 days shorter for left than for right members of each pair of teeth. This also is statistically significant in aggregate. The compensatory effect of quicker growth after later eruption of left teeth resulted in their reaching full size about a week after right teeth.

As a measure of symmetry, the age at eruption of the left tooth was subtracted from that of the right. To determine whether heredity governed this expression of symmetry, the 'right-left' value for one member of each twin pair was subtracted from the 'right-left' value obtained from the other member. The within-pair variance was then calculated from the differences in these values. This variance from MZ twins was only about half that obtained from the DZ twins for the 1st and 2nd incisors. For 3rd and 4th incisors the variance from MZ twins was slightly greater than that from DZ. Within-pair variances from HZ were less than those from DZ pairs for 1st and 2nd incisors but appreciably larger for 3rd and 4th incisors.

The observations would be consistent with some degree of genetic control. There might be in addition some 'right-left' asymmetry in individuals due to observational bias or to the direction of movement of the lower jaw in chewing.

Sources of variation in age at eruption

Although the total variation in each of the three groups of animals was much the same, the three fractions into which it has been divided for each group are neither equal nor consistent. In terms of mean squares, the within-animal variation (that is, variation within a given pair of teeth) is relatively small and similar for all groups. It tended to increase slightly from 1st to 4th incisors. This agreement of the three groups is to be expected but ceases at this point. Whereas one member of an MZ pair agreed with the other as well as one tooth did with its mate, DZ twins on average differed noticeably for all teeth. HZ pairs showed still more intra-pair variation; as they should on genetic grounds. What the MZ twins lacked in variety within pairs they more than made up in differences between pairs. In this respect they exceeded both DZ and HZ pairs—a distinction they may have owed to an original genetic sampling diversity. Of these generalizations, which are based on the facts given in Table 3, the most interesting relates to the apparent failure of any accidents of environment to make MZ twins any less alike than right and left sides of the same animal. Such accidents seem to have been of no importance at all in MZ twins nor, by inference, in DZ and HZ pairs.

Heritabilities may be calculated from the within-pair variances in Table 3 on assumptions set out by Donald (4) and modified by King & Donald in the paper on growth (7). Briefly, variation arising within MZ pairs is thought of as entirely environmental (e'^2); variation arising within DZ pairs contains the whole of e'^2 and half the additive genetic variance ($\frac{1}{2}g'^2$), and that within HZ pairs the environmental component (e'^2), three-quarters of the additive genetic variation ($\frac{3}{4}g'^2$), and a component m'^2 containing variance not otherwise accounted for. Heritability (h^2) is then taken to be the ratio of the genetic variance (g'^2) to the total variance ($g'^2+e'^2+m'^2$). The argument can be simplified by assuming that the variance arising within HZ pairs contains only $e'^2+\frac{3}{4}g'^2$; the e'^2 from MZ twins is then assumed to be applicable to half-sibs. This, however, may be too risky an assumption to make. The HZ variance has, therefore, been

regarded as containing an m'^2 component which has been isolated by deducting estimates of e'^2 and $\frac{3}{4}g'^2$ obtained from the twin data. Table 4 in line (*a*) gives estimates of heritability where e^2_{HZ} is assumed to differ from e^2_{MZ} and e^2_{DZ} by this component m'^2. These estimates are markedly different from those in lines (*b*) and (*c*) of Table 4 where the presumption holds that $m'^2=0$. Line (*b*) is derived from twins only. Line (*c*) shows the results of assuming $m'^2=0$ and using MZ, DZ and HZ intra-pair variances to yield two separate estimates for both e'^2 and g'^2. These have been combined by the least squares procedures into single estimates from which the ratio h^2 has been derived. The intra-class correlation of MZ pairs is sometimes used as an estimate of heritability (line (*d*)) on the assumption that environmental variation in one-egg twins is the full measure of this variation in unrelated animals.

Table 3. *Analysis of variance of age at eruption of permanent incisors in twins and half-sibs*

	Incisors							
	1st		2nd		3rd		4th	
Source	DF	MS	DF	MS	DF	MS	DF	MS
	One-egg twins (MZ)							
Between pairs	14	73·9	12	77·0	10	195·6	7	303·3
Within pairs	15	1·3	13	1·1	11	1·7	8	3·7
Within animals	30	0·8	26	1·1	22	3·1	16	1·8
	Two-egg twins (DZ)							
Between pairs	13	40·7	11	70·8	9	100·0	6	91·8
Within pairs	14	12·4	12	10·8	10	32·5	7	29·3
Within animals	28	1·5	24	2·8	20	1·7	14	2·8
	Half-sibs (HZ)							
Between pairs	12	41·2	11	30·9	10	66·6	8	79·9
Within pairs	13	11·6	12	18·1	11	86·8	9	123·5
Within animals	26	1·0	24	1·4	22	4·8	18	4·5

Table 4. *Heritabilities of age at eruption of incisors*

	Incisors			
h^2 calculated from:	1st	2nd	3rd	4th
(*a*) MZ, DZ, HZ	1·29	0·85	0·60	0·38
(*b*) MZ and DZ only	0·94	0·95	0·97	0·93
(*c*) Least squares method (MZ, DZ, HZ)	0·90	0·95	0·98	0·95
(*d*) Intra-class correlation of MZ	0·96	0·97	0·98	0·97

The heritabilities in Table 4 are likely to be slight overestimates to the extent that variance due to dominance, epistasis and genotype-environment interactions are included in g'^2 (7). However, the estimates in lines (*b*), (*c*) and (*d*) are so high that, even assuming some error due to these causes, there appears little scope for non-genetic variation. These possible errors will have relatively little effect on the age trend in h^2 in line (*a*); this will be further discussed below.

Correlation between age at eruption of successive teeth

Eruption of successive teeth may well be part of a single process in which all the events are interdependent. Correlations and partial correlations, to measure the degree of any such interdependence, have been calculated only from animals with complete records on

all four pairs of permanent incisors, viz. 14 MZ, 14 DZ and 18 HZ (i.e. two fewer than the forty-eight animals with 4th incisors shown in Table 2—by reason of an incomplete record for the 3rd pair of teeth of two of the MZ twins).

Table 5. *Correlations and partial correlations between ages at eruption of pairs of permanent incisors*

Tooth pairs held constant	Correlation or partial correlation for pairs					
	1 : 2	1 : 3	1 : 4	2 : 3	2 : 4	3 : 4
—	0·63	0·47	0·59	0·82	0·75	0·83
1	—	—	—	0·76	0·60	0·77
2	—	−0·09	0·23	—	—	0·56
3	0·47	—	0·40	—	0·22	—
4	0·35	−0·03	—	0·54	—	—
1 and 2	—	—	—	—	—	0·60
1 and 3	—	—	—	—	0·04	—
1 and 4	—	—	—	0·59	—	—
2 and 3	—	—	0·34	—	—	—
2 and 4	—	−0·27	—	—	—	—
3 and 4	0·43	—	—	—	—	—

Had all the animals concerned been unrelated, all coefficients in Table 5 above 0·3 would have been significant at the 5% level of probability. Since the animals had various degrees of relationship, the 5% significance level will lie between 0·3 and 0·4. The corresponding values for 1% significance are 0·4 and 0·5. The outstanding features of the correlations are the comparatively high values for adjacent pairs and the lowering of the correlation between pairs when the age of eruption of intervening pairs is held constant. The negative partial correlations between pairs 1 and 3 are non-significant and are probably sampling deviations from zero.

Holding constant the age at eruption of the 1st pair of incisors appears to have little effect on the correlations between the other three pairs of teeth. Pairs 2–4 seem to form a group within which pairs 2 and 4 are equally correlated with pair 3 and not correlated with each other except through 3.

Kemball (6) has indicated that in humans if pregnancy occurs at an age prior to the eruption of the third molars the eruption of this pair appears to be accelerated. In the twin data, eruption of first and third pairs of teeth took place shortly before first and second calving respectively. There is, for the forty-six animals included in Table 5, a positive correlation of about 0·4 between age at eruption of the first pair of incisors and age at first calving and a similar correlation between the age at eruption of the third pair of incisors and age at second calving. There is no correlation between either of the two ages at calving and age at eruption of the second or fourth pairs of teeth except that expected through their direct correlation with other tooth pairs. The data therefore are in accordance with the idea that a higher metabolic rate during pregnancy (10) may speed dental development. The correlations of age at eruption with aspects of performance such as pregnancy may, in some measure, explain the relationships in Table 5.

Relationship between body weight and age at eruption

It has been claimed that beef breeds develop their incisors at an earlier age than dairy-type animals. The animals available in the present experiment were all on the same management, but were of a large variety of breeds and crosses that prevented a direct

partition of the data by breed types. However, body weight at a particular age will in part be a function of breed type as will the increase in weight over a fixed period of time. Accordingly, age at eruption of the 1st pair of incisors was correlated with weight at 18 months of age, and time between the eruption of 1st and 4th pairs of incisors with weight increase between 18 and 42 months. The results are shown in Table 6.

Table 6. *Correlation between body weight and age at eruption of incisors*

	(*a*) Weight at 18 months and age at eruption of 1st incisors		(*b*) Weight difference (42 – 18 months) and age difference (4th – 1st incisors)	
Group	No. of animals	*r*	No. of animals	*r*
MZ	30	−0·20	16	−0·22
DZ	28	−0·30	14	+0·19
HZ	26	−0·15	18	−0·26
All	84	−0·19	48	−0·10

The correlation (−0·19) between 18 months' weight and age at eruption of the 1st pair of permanent incisors does not quite reach the 5% significance level and none of the correlations in part (*b*) of Table 6 are significant. Nevertheless, the three groups in part (*a*) agree in suggesting that the heavier the animal at 18 months of age, the earlier the 1st incisors erupt. There is less evidence for a relationship between gain in weight and age difference between first and last teeth. But for the behaviour of the DZ group it could have been concluded that the more weight gained in the 2 years following 18 months of age, the shorter is the interval between eruption of first and last teeth.

If beef animals mature more quickly than dairy types and if any of the above weight relationships are a function of maturity, then the correlations are at least in the direction expected.

Interval between Eruption and complete Emergence

The data on this aspect of incisor development were analysed in the same manner as the data on age at eruption. Table 7 gives the mean intervals between eruption and complete emergence for the four pairs of incisors.

Table 7. *Interval between eruption and complete emergence*

Incisor pair	No. of animals	Mean interval (weeks)	Mean square of interval
1st	84	5·9	2·30
2nd	74	4·4	0·85
3rd	64	5·3	1·59
4th	42	9·8	7·61

The mean interval for the first three pairs of incisors between eruption and complete emergence was about 5 weeks with a standard deviation for each pair of a little over 1 week. The length of time the 4th pair took to come fully up, however, was nearly double that of the earlier teeth. The mean square for this pair (7·6) was also much greater. In some other mammals and in humans the canine teeth (i.e. the 4th pair of 'incisors' in cattle and sheep) also take longer to grow both before and after eruption than the three pairs of incisors (18). At the age of $3\frac{1}{2}$ years when in cattle this pair emerges, bone growth around the tooth has by no means ceased. Skeletal growth, however, has become very slow at this age and the behaviour of the 4th incisors accords with this fact.

Correlations between the times taken by successive pairs of teeth to emerge fully were all less than +0·5. But as before, the strongest correlations were between the second and third pairs of teeth and between the third and fourth; these were but little affected by holding constant the values for the other pairs of teeth. Correlations between pairs that were not adjacent were due almost entirely to correlations with intervening pairs of teeth.

An analysis of variance of these data showed that the smallest part of the variance was due to differences between left side and right side—although the proportion of this to the total variance was appreciably greater than for age at eruption. With the exception of the value for the 4th incisors of HZ cows, the mean squares within animals were consistent for both groups of twins and the half-sibs, eight of twelve values falling between 0·40 and 0·59. Variances between pairs were larger than those within pairs in most cases, but significantly so in less than half of them. The within-pair mean squares were greater, by and large, for DZ and HZ than for MZ pairs, but not in the striking way shown by age at eruption. If there is any effect of heredity on rate of emergence, it is small.

DISCUSSION

Variation in age at eruption of incisors reduces their value for determining age. Some animals have their second pair of teeth before others have erupted their first. One animal among the twins discussed even had a third incisor before a number of others had had their first. None of the twins in the present study had cut their 1st permanent incisors nor had their second pair fully up (or even cut) at the age suggested in the Smithfield rules. On the other hand, nine animals had cut their 3rd pair of incisors before 2 years 8 months—the stipulated age—one of them by as much as 14 weeks. Only one of the half-sibs had a 4th pair of teeth fully emerged before the age of 3 years, but the state of the anterior molars, also considered under Smithfield regulations at this age, is not known. Under the rules, an exhibitor may prove the age of his beast when its dentition is not in accordance with expectation, and this no doubt will meet most contingencies.

If this study had been made only on twin data, it would have seemed clear that such uncontrolled differences as there were between the two environments of a pair of twins reared together had a negligible effect on the age at which the several incisor teeth appeared. One-egg twins resembled each other as closely as right and left sides of all animals, whereas two-egg twins kept along with them were significantly less concordant. Both kinds of twins differed markedly from pair to pair, no doubt as a result of genetic differences between pairs. Such differences were augmented perhaps by environmental factors that assumed importance in comparisons of animals born as much as 8 months apart. In a population of animals born on the same day, reared together uniformly and characterized by a genetic variation twice that found within DZ pairs, 90% or more of the observed variation would have appeared to be genetic. Had this been the whole truth, however, the variance within HZ pairs ($e'^2 + \frac{3}{4}g'^2$) should have been just $\frac{1}{4}g'^2$ larger than the variance for DZ pairs for each of the four pairs of teeth. In fact there was a discrepancy, m'^2, too large to be ignored, although in no case significant. The relative magnitude of m'^2 increased with time.

If the estimate of e'^2 and g'^2 (from twins) and m'^2 (from HZ pairs) are summed, and each expressed as a percentage of the total, as has been done in Table 8, the changes in m'^2 relative to e'^2 and g'^2 can be easily followed. For the first incisors, m'^2 was negative because

the HZ pairs were unexpectedly less variable (within pairs) than DZ pairs. Large standard errors attaching to the values of m'^2 allow this, and indeed the remaining values of m'^2, to be attributed to sampling error. The time trend which results in m'^2 amounting to 60% of the total variance for the 4th incisors is, nevertheless, suggestive of a meaning for m'^2 beyond its content of sampling errors; otherwise these errors have to be supposed to increase in an orderly fashion. This is not impossible, especially since numbers of animals were culled during the course of the observations, though for reasons unrelated to teeth. It may be recalled, however, that estimates of m'^2 from data on the growth of all animals up to 18 months of age were also rather too large to be overlooked (7). Demands on sampling errors become more heavy to sustain than those on the hypothesis that m'^2 measures a real departure from the postulate that e'^2 and g'^2 account for all variation and can be added together.

Table 8. *Estimates of e'^2, g'^2 and m'^2 expressed as percentage of their sum*

	Incisors			
	1st	2nd	3rd	4th
% e'^2	7·8	4·9	1·7	2·7
% g'^2	129·1	84·7	60·3	37·6
% m'^2	−36·9	10·4	38·0	59·7

It is difficult to suppose that m'^2 for 4th incisors has much to do with immediately pre- or post-natal effects. A more likely explanation is that it is due to a kind of genotype-environment interaction. Although superficially exposed to the same environment, all animals in this experiment had some degree of choice in respect of its components (for instance when at grass) and their own individual reactions to such of those components as were constant for all. The results are readily conceived to be cumulative so that m'^2 would increase with time. HZ pairs, being more genetically unlike, would vary most in their reactions. DZ twins would vary less, but all variation from this cause would be inseparable from additive genetic variation and would help to inflate the estimates of heritability to the high observed values. Consequently, m'^2 obtained by comparing MZ and DZ with HZ pairs is possibly an underestimate of this type of variation to the extent that e^2_{DZ} is greater than e^2_{MZ}. At present there is no direct evidence of the magnitude of e^2_{DZ} in cattle.

In human twins, e^2_{DZ} may in fact be less than e^2_{MZ}. Intra-pair variation in human monozygotic twins attributable to vascular anastomosis is claimed to be often such as to cause individual differences greater than those in dizygotic pairs where anastomosis does not occur (2). The result of ignoring this would be to underestimate the importance of heredity. This primary bias is unlikely to have a similar disturbing effect in studies of cattle twins since the great majority of dizygotic twins establish vascular anastomosis (1).

It is a relevant question whether or not the same pairs of animals contribute proportionately similar amounts to the variance of the different characters studied. The characters themselves are very likely to be dependent on each other as different pairs of incisor teeth have been shown to be, or as height and weight are. Pairs of animals, therefore, which for any reason acquire a comparatively large difference in one respect may well acquire a large difference in another.

Several considerations demand further study of this subject. The immediate problem

is how far it is justifiable to regard the evidence for the existence of m'^2 presented in this paper as confirming the earlier evidence (7) based on the growth rate of the same animals. The correlations between growth rate and age at eruption of incisor teeth given above are small and non-significant and it could therefore be held that the two bodies of evidence for m'^2 are together much stronger than either taken alone. Just how much stronger they are in combination with each other or with further evidence from the same animals depends on a more precise knowledge of the correlations between the characters studied than is yet available.

SUMMARY

1. Data are presented on variation in age at eruption of permanent incisor teeth in one-egg (MZ) and two-egg (DZ) twins and in pairs of half sisters (HZ). The 1st pair of incisors erupted when animals were on average 100 weeks old and the other three pairs came at roughly 26-week intervals thereafter. Variation in age at eruption increased from 1st to 4th incisors, but the coefficient of variation remained constant at about 8%. The mean interval between eruption and complete emergence was about 5 weeks for the first three pairs of teeth and nearly 10 weeks for the 4th pair.

2. Variation in age at eruption within MZ pairs was no greater than that between left and right sides of the same animal. DZ displayed greater within-pair variances than MZ twins, and HZ pairs greater than DZ.

3. Correlations of age at eruption of teeth with body weight and with gain in weight were negative but non-significant. Age at eruption of 1st and of 3rd teeth was positively correlated with age at 1st and 2nd calving, but eruption of 2nd and of 4th teeth was not.

4. For 2nd, 3rd and 4th incisors, the intra-pair variance of the HZ group was in excess of that expected. This can be interpreted to mean that the estimates of environmental and genetic variation derivable from MZ and DZ pairs are not adequate to account for all the variation within HZ pairs.

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THE INFLUENCE OF FOUR LEVELS OF FEEDING ON THE POSITION AND ERUPTION OF INCISOR TEETH IN SHEEP

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Farmers examine the teeth of their sheep not only to determine or check age, but also to make sure that each sheep is properly equipped for grazing. A hill sheep, in particular, needs a good set of teeth to enable it to thrive. When its teeth begin to fail it is culled for 'broken mouth'. To be good, the teeth must be individually healthy, the molars must fit accurately together and the incisors must meet the maxillary pad in a position which will allow the sheep to grasp its food. The position of the incisors was found by Hitchin (1948) to vary in samples of sheep from different breeds. He found that the incisors of Blackfaces met the middle of the pad, those of Cheviots the anterior part and those of Border Leicesters protruded in front of the pad.

In the literature (reviewed by Donald & Wiener, 1954) there is evidence for inheritance of the more extreme jaw defects. Little, however, seems to be known of the source of minor variations in cattle or sheep. In fact, no measure of such variation has come to our notice, although Nordby, Terrill, Hazel & Stoehr (1945) measured the skulls of both 'normal' and 'overshot' sheep. They found that the latter had both longer skulls and shorter mandibles than had normal animals; also that the angle of the incisors could vary to compensate in part for minor jaw inequalities in 'normal' but not in 'overshot' sheep. Mating tests with defective and normal sheep led to the conclusion that several pairs of genes were involved. In earlier papers, Nordby (1931) and Muir, Deakin, Macmillan & Freeborn (1937) had advised how to eliminate jaw defects on the assumption that recessive genes were responsible.

An opportunity to study the matter was presented recently by an experiment in which two breeds and five crosses of sheep were subjected to four different feeding treatments. Details of the design will be reported by King, Watson & Young (1956). We propose to say just enough about it to explain the observation on the teeth and the analyses attempted in this paper.

EXPERIMENTAL MATERIAL

The sheep consisted of seventy-five pairs of twin lambs composed of nearly equal numbers of each of seven breed types, being the offspring of Blackface ewes by Wiltshire, Border Leicester, Lincoln or Blackface rams, and Welsh ewes by Welsh, Wiltshire or Suffolk rams. The Welsh and Blackface ewes with their lambs each derived from several flocks, but all the Welsh were brought together on to one farm and all the Blackfaces on to another soon after lambing. This was designed to minimize environmental differences within the Welsh and the Blackface blocks of sheep. The two breed blocks were united in September 1953, and the experiment with different feeding treatments started in October. Differences arising between the two blocks will be attributable to breed of dam, to early environment, and to the fact that the sheep born to Welsh ewes were on average a month older than those born to Blackface ewes.

The feeding treatments covered a period of 7 months lasting until May 1954, when the animals were a little over 1 year old. Throughout the experiment there was a high and a low plane of nutrition produced by different rates of pasture stocking and by feeding supplements to the high-plane animals. On the high plane the animals were in a constantly improving condition, while on the low plane their final weight was about the same as their initial weight. For the first 4 months, half the twin pairs were split between the high and low planes of nutrition. The remaining pairs were left unsplit and assigned in equal numbers to each treatment. For the next 3 months half the animals on each plane were switched to the other plane of nutrition, thus creating a set of four treatments, viz. low-low, low-high, high-low and high-high. With one-half of the twin pairs split at the beginning of the experiment and the other half split at the time of the change-over, only one member of each pair could appear in any one of the four final treatment groups. Ewe and wether lambs were allocated at random to the four treatments. Any possible differences between the sexes have been ignored in the comparison of the influence of breed and treatment on the characters studied here.

PRELIMINARY OBSERVATIONS

The teeth were examined towards the end of January 1954, just prior to the change-over when the sheep had been on either the high or low plane of feeding for 4 months. The position at which the

central incisors met the maxillary pad was graded directly by eye. Observations showed that the modal position, which was graded zero, was the anterior third of the flat part of the pad. Positions anterior to this were called negative, and posterior positions positive. The flat part of the maxillary pad was divided into three approximately equal sections, graded 0, +1 and +2. Occlusion with the anterior upward-sloping part of the pad was graded −1. Other grades were employed when necessary.

The distribution of the *incisor bite grade* (as we have called it) is given in Table 1, according to the plane of nutrition. These results are suggestive of differences between Blackfaces on the two planes of nutrition and also between the Blackface block on the one hand and the Welsh block on the other. The three extreme animals graded +3 were all pure Blackface and two were twin to each other; the third was twin to an animal of zero grade. None of the three survived to the end of the experiment.

Table 1. *Distribution of incisor bite gradings of sheep on low and high planes of nutrition according to breed of dam (January 1954)*

Plane	Offspring of	−1	0	+1	+2	+3	Total	Average
Low	Blackface dams	1	29	10	—	2	42	+0·36
	Welsh dams	2	29	—	—	—	31	−0·06
High	Blackface dams	5	30	5	—	1	41	+0·07
	Welsh dams	3	27	3	—	—	33	0·00
Total		11	115	18	—	3	147	+0·11

Table 2. *Average incisor bite measure of 140 sheep (about 1 year old) according to breed and treatment (May 1954)*

	Treatment				Average of all treatment groups
Breed type (dam × sire)	Low-low	Low-high	High-low	High-high	
Blackface × Wiltshire	42·0	40·8	39·7	18·5	35·3
Blackface × Border Leicester	36·2	27·3	27·2	28·8	29·9
Blackface × Lincoln	41·2	29·6	28·1	19·1	29·5
Blackface × Blackface	33·6	28·8	27·9	21·5	28·0
Average of all Blackface groups	38·3	31·6	30·7	22·0	30·7
Welsh × Welsh	28·2	21·0	24·3	18·3	23·0
Welsh × Wiltshire	29·7	20·9	24·6	12·4	21·9
Welsh × Suffolk	27·5	20·3	24·1	12·3	21·1
Average of all Welsh groups	28·5	20·7	24·3	14·3	22·0
Average of all groups	34·1	27·0	28·0	18·7	27·0

Members of twin pairs were no more alike in bite grade than pairs of animals chosen at random, perhaps mainly because the great majority of gradings were zero. Thus for any detailed analysis it was necessary to have a more accurate measure of the variation in bite.

LATER OBSERVATIONS

(*a*) *Methods.* With the collaboration of Mr D. M. Watt of the Edinburgh Dental School a technique was developed for making plaster casts of the incisor teeth biting on the maxillary pad. These casts were then available for more leisurely and accurate observation than was possible on the live animal. The procedure involved covering a 3 in. watch-glass with softened plasticine (about 1½ in. thick) and pressing this firmly against the front of the sheep's closed mouth—having first parted the lips. A plaster cast was then made from each impression.

Impressions were taken early in May 1954, just before the feeding treatments were ended, from 140 sheep—that is seven fewer than were observed in January, because the three extreme animals (graded +3) and four others had died in the interval. The horizontal distance between the front of the maxillary pad of gum and of the front of the central incisors was measured on each plaster cast on two separate occasions. We have called this distance the *incisor bite measure*. A pair of sliding calipers reading to $\frac{1}{10}$ mm. was adapted for this measurement (cf. Nordby, 1935).

(*b*) *Results of incisor bite measurement.* The measurements ranged from zero (front of incisors in line with front of pad) to a value of 66 units (one unit $=\frac{1}{10}$ mm.), with a mean value of 27 units. The average difference between duplicate measurements was 4·0 units. The average difference between the ewe and wether hoggs (calculated within breed and treatment) was quite insignificant (wethers having a bite measure of 0·4 unit greater than ewes). The results are shown in Table 2 for the twenty-eight breed-treatment groups which each contain an average of five sheep. The highest mean value (42·0) was found in the Blackface × Wiltshire cross on the low-low treatment and the smallest mean value (12·3) in the Welsh × Suffolk cross on the high-high

treatment. By and large we found that the sheep in the Blackface block had teeth meeting the pad farther back (average value 30·7 units) than those in the Welsh block (22·0). This difference of 8·7 units was not, however, as great as that produced by the treatments. Animals in the high-high group with a mean measurement of 18·7 had teeth appreciably farther forward than those in the low-low group with an average bite measurement of 34·1, a difference of 15·4 units. The animals whose feeding régimes were switched have, in all cases but one, bite measures intermediate between the two extremes, but a small interaction is apparent here. All the low-high groups have a greater bite measure than the high-low groups in the Blackface block, but the reverse is the case in the Welsh block. The breeds in Table 2 have been arranged in order of their bite measurements averaged over treatments.

there is no satisfactory test of the breed × treatment interaction, it is interesting that the interaction variance (28·8) is much smaller than that between sheep (164·1). This suggests that twins may be more alike in bite measure than pairs of animals taken at random. Such could be due to maternal influence or to a degree of inheritance of bite measure or both. These various comparisons certainly do not provide conclusive evidence for genetic variation in the character studied, but neither do they rule it out.

In contrast, the treatments had clear-cut effects, highly significant when the variation was tested against the interaction term (Table 3). Moreover, the treatments appear to have acted additively, and as far as the observed end results on bite measure were concerned, it seemed not to matter whether high treatment followed the low, or low treatment followed the high.

Table 3. *Analysis of variance of incisor bite measure and correlations of bite measure with body weight (r_{mw}), May 1954*

Source of variation	D.F.	M.S.	F	r_{mw}
Between breeds	6	214·6	1·31	+0·685
Between blocks	1	1032·6	6·29*	+1·000
Within blocks	5	51·0	0·31	+0·176
Between treatments	3	558·5	19·66**	−0·960**
First half	1	719·3	25·33**	
Second half	1	938·9	30·05**	
Interaction	1	17·3	0·61	
Interaction: treatment × breed	18	28·4		−0·118
Between blocks	3	32·5		
Within blocks	15	27·6		
Within class				
Between sheep	112	164·1		+0·113
Within sheep between duplicate measurements	140	12·8		

* Significant at 5 % level. ** Significant at 1 % level.

Further analysis was directed primarily to testing the statistical significance of breed and treatment effects displayed by the average values in Table 2. An analysis of variance based on these average values is shown in Table 3. This table also gives the variation between individual sheep and the variation between duplicate measurements. The repeatability of measurements on casts was about 86 %.

Interpretation of the analysis (Table 3) is complicated by the fact that all twin pairs were split between treatments. Thus all differences between members of any pair are confounded with differences in treatment. Therefore, the breed variation was tested against the variation between sheep (within class), but it was found to be non-significant. However, the difference between blocks when taken out of the pooled data was significant. Of course, this difference may be due to a variety of causes: breed of dam, or pre-experiment differences in treatment or in time of lambing. While in this form of analysis

(c) *Relationship of incisor bite measure to body weight.* In May 1954, the Blackfaces and their crosses weighed on average 91 lb. and the Welsh and their crosses 76 lb. It was seen above (Table 2) that the former had the larger bite measure, so that there is a positive correlation between breed means of weight and bite measure. The sheep on the high-high treatment, however, had appreciably smaller average bite measures than the sheep less well fed, although the sheep in the former group weighed on average 103 lb., and those in the low-low group 65 lb.; in other words, there is a negative correlation between the treatment means of weight and bite measure. The values of these correlations are shown in the last column of Table 3. The between-breeds correlation (+0·685), unlike that between treatments (−0·960), is not statistically significant. Since these opposing trends might well cancel, it is to some purpose to consider what happens to the relationship between bite measure and body weight

for any one breed type on a given level of feeding. This correlation was found to be small (+0·113) and not statistically significant, but we have reason to believe from other unpublished evidence on sheep of similar age that a within-class correlation of this magnitude is real.

(*d*) *Observations on eruption of permanent incisor teeth.* According to Brown (1949) sheep usually cut their central permanent incisor teeth soon after 1 year old and have them fully up at 15 months. The Smithfield Rules (1954) state that sheep with permanent central incisors cut will be considered as exceeding 10 months of age. On both criteria our sheep would have been correctly aged. When the casts were made early in May 1954, and the sheep were between 11 and 14 months old, a few sheep in the high-high group were cutting permanent central incisors; these sheep were chiefly of the Wiltshire × Welsh cross. further 28 % lacked deciduous teeth and would presumably have shown permanent teeth had they been seen 18 days later.

Whereas there were differences of treatment before the experiment began between the Blackface and Welsh blocks and differences in mean age, as already noted, there was little such variation within each block. Thus an obvious indication of breed influence is seen in the relatively large proportion of permanent teeth erupted in the Wiltshire crosses both with Blackface and Welsh ewes. In the Wiltshire × Blackface crosses, 46 % of sites showed permanent incisors compared with an average of 20 % in the other Blackface crosses. Amongst the Welsh, the difference is even greater—nearly all (98 %) of the expected permanent central incisors had erupted in the cross with Wiltshire, but only 19 % on average in the others.

Table 4. *Percentage of central permanent incisor teeth which had erupted in* 140 *sheep (about* 1 *year old) according to breed and treatment*

	Treatment				
Breed type	Low-low	Low-high	High-low	High-high Observed 30 May 1954	Average of all treatment groups
	Observed 17 June 1954				
Blackface × Wiltshire	33	75	75	0	46
Blackface × Border Leicester	17	60	40	17	33
Blackface × Lincoln	0	10	10	33	13
Blackface × Blackface	0	33	20	0	13
Average of all Blackface groups	12	45	36	12	26
Welsh × Welsh	17	20	17	17	18
Welsh × Wiltshire	90	100	100	100	98
Welsh × Suffolk	20	0	25	33	20
Average of all Welsh groups	42	40	47	50	45
Average of all groups	25	43	41	29	34

The sheep in the high-high group were re-examined on 30 May immediately prior to slaughter, but the animals in the other groups were not re-examined until 17 June. Substantial proportions of sheep in each treatment group had their permanent teeth up, though sheep on the low-low feeding had fewer than those better fed. The percentage of central permanent incisors erupted (Table 4) was 25 for the low-low group, 43 and 41 for the low-high and high-low groups respectively. We have assumed that the proportion in the high-high lot, had they been observed at the same time as the other groups, instead of 2½ weeks earlier, would have been around 60 %, if not more. This assumption is based on three lines of evidence: (1) large numbers of eruptions had occurred in all treatment groups in the 3–5 weeks between making the casts and re-examining the mouths; (2) there is supporting evidence on the rapid emergence and growth of permanent incisors in cattle (Wiener & Donald, 1955); (3) on 30 May, in the high-high groups, 29 % of the sites of central incisors were occupied by permanent teeth, while a

DISCUSSION

The only clear-cut and significant effect on incisor bite measure was that of the treatments. This is interesting because of the inference to be drawn from the literature that heredity plays an appreciable part in bite variation. We think, therefore, that it may be necessary to make a distinction between the extreme defects most often described (such as those also displayed by three of our animals that died) and the more limited variation observed in the majority of our sheep. While the former may be inherited quite simply, our present evidence for genetic variation of the latter is inconclusive, but the response to treatment is obvious.

We have no evidence on the question whether these treatment effects resulted from the undoubted differences in food-energy intake of the sheep or from other factors such as food texture or mode of grazing. However, it seems to us that the energy intake was probably the most important treatment factor in this experiment. Similarly, we do not know

whether the treatment differences caused variation in the growth of mandible or maxilla, affected pad width, or angle of teeth, or a combination of these and other variables.

The small absolute size of the treatment differences (as distinct from the significance of the effect) may be no more than a reflexion of the short duration of the experiment. The interesting feature is that the better the feeding the smaller the bite measure. Hitchin (1948) observed that Border Leicester sheep had incisors much farther forward in relation to the pad than Blackface sheep. Since Border Leicesters are normally associated with good feeding conditions and Blackfaces with more austere environments, this difference in incisor bite measure may be a consequence of extended differences in treatment. The fact that the sheep associated with the poorer environment had the bigger bite measure agrees with our experimental findings.

In respect of the percentage of deciduous incisors which had been replaced by permanent teeth when the sheep were between 12 and 15 months old, the treatment effects were marked—the better the feeding the higher the proportion of replacements. However, the difference between the Wiltshire crosses and their contemporaries points also to some measure of genetic control of time of eruption of the first permanent incisors. This is in line with studies on cattle (Wiener & Donald, 1955) which showed that age at emergence of permanent incisor teeth was subject to considerable heritable variation.

For both incisor bite and time of eruption of the central permanent incisors, the treatments seemed to be roughly additive in the effects they produced. Whether such effects accumulate throughout an animal's lifetime and whether they persist or not are problems we are now studying in other data.

SUMMARY

The distance between the front of the incisor teeth and the front of the maxillary pad (incisor bite measure) was measured in 140 sheep about 1 year old. The sheep consisted of seven breed types—the offspring of Blackface ewes by Wiltshire, Border Leicester, Lincoln and Blackface rams, and of Welsh ewes by Welsh, Wiltshire and Suffolk rams. Within each breed type the effects of four different feeding treatments lasting 7 months were studied. These produced small but very significant differences in bite measure. Differences between breed types were significant only in respect of the division between the two breeds of dam. Effect of breed of dam, however, was confounded with any effect due to differences in origin.

The proportion of permanent central incisors which had replaced milk teeth when the animals averaged a little more than a year old was affected both by the level of treatment during the experiment and by breed.

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GROWTH OF CATTLE TWINS ON DAIRY FARMS WITH HIGH AND LOW YIELDING HERDS

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IN 1950, the Animal Breeding Research Organisation started an experiment aimed at increasing knowledge on three questions:

(1) How much of the difference in milk yield between herds of the same breed is due, on average, to genetic differences and how much to environmental ones?

(2) If different levels of herd yield reflect different farm environments, will these environments affect the growth of the animals, and if they do, is there any correlation between the effects on growth and those on yield?

(3) What sort of differences of natural environment and of management are associated with differences in average yield of dairy cattle on different commercial farms?

The Experiment was designed and in its early stages supervised by Drs. J. M. Rendel* and A. Robertson†. The design consisted of choosing a number of farms with high-yielding herds and an equal number with low-yielding herds—on the basis of herd average—and of placing week-old twins, one member of each pair into each yield group. Two-egg twins were used because, by comparison with one-egg twins, they were more readily available and would make up with numbers any disadvantage in statistical efficiency.

A comparison of the difference in yield between the split twins with the difference between the herd averages would give useful information on the first question. Body measurements on the twins would allow the study of growth. The nature of any environmental differences between the chosen farms would be gauged from a study of factors involved.

The experiment is now complete as far as the collection of data on growth is concerned and it is this aspect which is considered in this paper.

MATERIAL AND METHODS

Sixty-five pairs of female two-egg twins were purchased over a three-and-a-half-year period beginning in the autumn of 1950. The calves were of pure Ayrshire, Friesian or Dairy Shorthorn breeding (though not necessarily registered in a herd book). They were placed on farms in the West Midlands of England which carried dairy herds of the same breed type. Each pair of twins was bought and placed out within a week of birth, and split at

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random between a farm having a relatively high-yielding herd (*A*) and one having a lower-yielding herd (*B*). All herds were milk recorded, initially at any rate.

The average herd yields for the cows of the three breeds and two yield groups were approximately as follows:—

TABLE 1

Average herd yields (cows only) at time of farm selection

	A (high)		*B* (low)	
	No. herds	Yield (gal.)	No. herds	Yield (gal.)
Ayrshire	26	900	26	640
Friesian	24	1,100	24	700
Shorthorn	15	800	15	605

These average yields refer to a single milk recording year one or two seasons prior to placing out the twins. For any pair of herds, the yield difference may be greater or smaller than the average, but within each breed there is virtually no overlap in yield between *A* and *B* herds.

The twins were reared by the co-operating farmers along with calves of their own and given no special attention. Our evidence suggests that the twins were, on average, treated in the same way as other cattle of similar age on the same farms. No farm had more than one twin at any one time, though twins lost in the early stages of the experiment were, in a few cases, replaced.

Twins were weighed and measured at 16 weeks old and measured at six-monthly intervals thereafter. A few of the twins were also weighed at the time of purchase. The following ten body measurements were taken on the animals:

Height at withers	Head length
Height at sacrum	Length of sacrum (pins to hooks)
Width at forerib*	Length from pins to shoulder
Width at pins	Depth of chest
Width at hooks	Foregirth†

Members of a twin pair were measured as nearly as possible within a day or two of each other. Not all twins were available for observation at each due date. Outbreaks of foot-and-mouth disease in the region prevented a considerable number of visits at the desired times: and losses, for a variety of reasons, of one or both members of a twin pair occurred at all ages. These factors have considerably reduced the data suitable for analysis. The measurements dealt with in this paper will refer only to complete pairs seen within two weeks of the appropriate age.

RESULTS

It is a basic assumption of the analysis that differences present at birth within twin pairs—that is between the members of a pair—were distributed at random. Thus, at the start of the experiment, there should have been

* Widest point on path between middle of 4th rib and top of 7th rib.

† Immediately behind forelegs and vertically up the sides.

no significant differences in the average size of the calves in the two groups. Confirmation of this comes from 25 unselected pairs of twin calves which were weighed at the time of purchase (within a week of their birth). The 25 twin calves allocated to the *B* (low) farms were found to weigh 0·8 lb. more on average than their co-twins destined for the *A* (high) farms. By the age of 16 weeks when the twins were first visited, appreciable differences had developed between those on the *A* and those on the *B* farms. Twenty of the pairs mentioned above were also weighed at 16 weeks old and those in group *A* had gained 124 lb. while their co-twins had put on only 110 lb. This demonstrates that the average differences in yield between the cows in these two groups of farms are associated with differences in the growth of the young stock. Whatever the nature of the environmental differences between the two groups these differences will, for convenience, be referred to as 'treatment' differences.

Sources of variation

Major concern in this paper is with growth differences arising between members of twin pairs from the two treatments as represented by the two groups of farms. There are, however, other non-random sources of variation which could be important. As already mentioned, three breeds are involved. Also, since twin pairs were purchased over a period of $3\frac{1}{2}$ years, there could conceivably be systematic seasonal differences in the usual sense of the word 'season' and also in the sense that different standards might have applied in the choice of animals offered for sale at different times. Both breed and 'season' effects may interact with the treatments. Differences between twin pairs due both to heredity and to environmental factors, including the farm of origin, obviously exist; interactions between pairs and treatments cannot, however, be recognised or estimated because all pairs were split between the two treatments.

For the first four or five measuring occasions (i.e. up to the age of 94 or 120 weeks) there appeared to be a sufficient number of pairs of twins to warrant division into categories for the purposes of a series of analyses of variance which would gauge the importance of the sources of variation mentioned. Such analyses were made on length of head, height at withers, length from pins to shoulder, and foregirth at five ages, and body weight at 16 weeks (a total of 21 analyses).

A simple ranking of the three breeds for the average growth differences of four body measurements at each of four ages, gave a hint that, on aggregate the Friesian twins displayed the greatest growth differences and Shorthorns the smallest—representing a slight but positive association with the average milk yield differences (Table 1) for the three breeds at the time of classification of the herds. However, the absence for each character at each age of a statistically significant breed $\times$ treatment interaction suggests that the three breeds responded similarly in their growth to the environmental differences between the *A* and *B* farms.

Grouping of the twin pairs according to year of purchase revealed no significant year effect on the growth differences. It would, therefore, appear that no systematic differences arose in the type of animals offered for sale over the $3\frac{1}{2}$ year purchasing period, or in the standards applied by the different field staff who were involved in the purchase and measurement of the animals at different times.

In view of the above findings, the data from the three breeds and the

several seasons were pooled for the purposes of subsequent analysis. Size differences between twin pairs were statistically significant in all the 21 analyses referred to. For this reason the analysis of treatment differences was carried out entirely within pairs in conformity with the intentions of the experimental design.

Treatment differences

The results showed three main trends:

(1) There were considerable (and statistically significant) differences in body dimensions and weight between the twins reared in the *A* and *B* groups. These size differences must have developed in consequence of some average treatment difference during rearing which in turn is associated with the milk yield differences between the two groups of farms at the time of classification.

(2) Most of the size differences had been established by the age of 16 weeks when the animals were first weighed and measured. The two groups continued to diverge, but at a lesser rate, for about another year. The differences then began to diminish, on average, although they had not disappeared by $3\frac{1}{2}$ years old.

(3) Not all body dimensions responded in the same way to the treatments. Differences, when viewed in relation to the mature size of each character, were of varying magnitude—changing not only with age but with the character. Differences between the groups tended to be smaller and to fade away earlier for some body characters than for others, and in such a way that the two treatments have resulted in animals of different conformation at the observed ages.

Since the body size differences were, on the whole, greatest at the younger ages, it is not surprising that the statistical significance of the differences also diminishes with age. Testing the significance separately for each of the ten linear body dimensions at each age, and for the total number of twins available each time, we find the following number of body size differences falling into each significance class:—

TABLE 2

The number of differences in linear body measurements significant at various levels—by age of twins

Probability of the difference being due to chance	Age at observation (weeks)							
	16	42	68	94	120	146	172	198
Less than 1%	10	10	8	5	5	—	1	1
1% to 5%	—	—	2	3	4	3	4	2
5% to 10%	—	—	—	1	1	3	3	3
Greater than 10%	—	—	—	1	—	4	2	4

Larger numbers of twins would have produced very little change in the levels of significance of the observed treatment differences.

The conclusions to be drawn from any one set of measurements will reinforce those to be drawn from any other only to the extent to which the separate observations represent independent events. The closeness of association between different body parts on the same animal differs, but

generally high phenotypic and genetic correlations have been reported by Touchberry (1951) and Blackmore, McGilliard and Lush (1958). From our observations, however, the conclusion is inescapable that general body size differs significantly between the animals of the two treatment groups up to about 2 years old, even although not all body parts show the same relative differences. Thereafter the significant differences are more restricted to particular characters. The single observations of an average weight difference, at 16 weeks, is highly significant ($P = 0{\cdot}1\%$).

The finer details of the picture can be drawn only in the face of some difficulties. The greatest of these is the random absence of many pairs of animals from many of the observation periods. Thus a pair might be measured at 16 weeks old and not again for a year or eighteen months, other pairs may start being measured only at say 10 months old, and so on. Measurement changes from age to age if based on all available observations each time would therefore include not only age variation but variation due to some change in the twin population on which the measurements were made. The long interval (6 months) between intended measurements made it undesirable moreover to interpolate for missing values.

Sixteen pairs were measured on all of the first five visits (at 16, 42, 68 94 and 120 weeks)—but only three pairs on all of eight occasions. In order to maximise the numbers which can legitimately be compared from one age to the next, differences within pairs of twins were analysed in a stepwise fashion; that is to say, only those pairs which were present on two successive occasions were considered. Thus, 43 pairs were measured both at 16 and at 42 weeks old, 40 pairs (of which 33 are included in the first 43) were present at both 42 and 68 weeks, and so on. The numbers thus pertinent to each measurement interval are:

Age Interval (wks.)	No. Twin Pairs
16-42	43
42-68	40
68-94	31
94-120	33
120-146	28
146-172	15
172-198	10

Using this procedure, evidence was collected on how the treatment differences changed with age for each of the ten body dimensions. Each step was represented as a percentage change. These percentage changes from one age to the next were then applied to the actual mean difference of all the twins measured at 16 weeks old (51 pairs)—the maximum number measured at any one age. In this way, a growth curve was built up for each of the ten body parts. However, in order to make differences from the ten linear dimensions roughly comparable to each other, each was divided by an estimate of its mature size. These estimates of size at maturity were supplied by St. C. S. Taylor (personal communication) and are based on 60 pairs of two-egg cattle twins kept in one environment by the Animal Breeding Research Organisation. The results, averaged for 9 of the 10 body measurements, are shown by the solid line in Figure 1; forerib width is the dimension excluded for reasons discussed below. It can be seen that at the age of 16 weeks almost two-thirds of the maximum divergence between

the 2 treatment groups had been reached. On average, differences between the twins continued to emerge for a further year and then to disappear gradually—though at the age of 198 weeks the differences, when averaged for the 9 characters, still represented about 1% of their mature sizes.

The other (broken) line in Figure 1 represents the equivalent situation for the 16 pairs of twins measured at each of the first 5 times (16-120 weeks). Differences between the twins in this sub-population rise more rapidly between 16 and 42 weeks but also diminish more rapidly after 68 weeks to a lower value at 120 weeks than that estimated for the 33 pairs represented at this age by the solid line. The main interest lies not in the precise values of the differences but in the general shape of the curves.

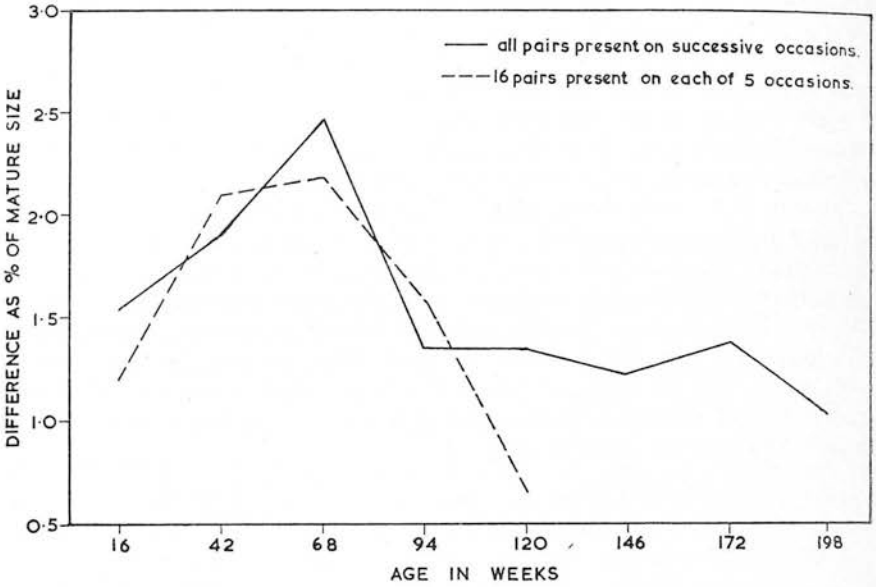

FIG. 1. Difference in growth, at different ages, of twins split between 'high' and 'low' yielding herds. The difference at each age is expressed as a percentage of mature size and averaged for nine linear body dimensions.

The measurement excluded from the average in Figure 1 is that of width at forerib and justification for the omission may be sought in Figure 2 which shows separately for each body measurement the differences between the twins on the *A* and *B* farms. Differences are expressed, as before, as a percentage of mature size for each character. Forerib width can be seen to show not just the greatest differences but also the greatest fluctuations—in particular 2 peaks, one at 94 weeks and a greater one at 172 weeks. Forerib width may well be thought to reflect more markedly than other characters any differences which exist in the body condition of the twins. Support for this hypothesis comes from the finding of St. C. S. Taylor, J. H. Watson and G. B. Young (personal communication) that forerib width was considerably more affected by feeding changes than any of eleven other linear body dimensions. The peaks in Figure 2 may represent special cases of such differences in condition, for at the 2 ages with which the peaks coincide (94 and 172 weeks) the twins in the two groups were as much as 7 weeks out of step with each other in respect of stage of pregnancy; at the two intervening times the twins were more nearly in step. Thus at 120 weeks the

animals in the *A* group were on average only 3 weeks nearer to calving for the first time than those in the *B* group, and at 146 weeks old the twins in both groups had, on average, calved, but were not yet pregnant for a second time.

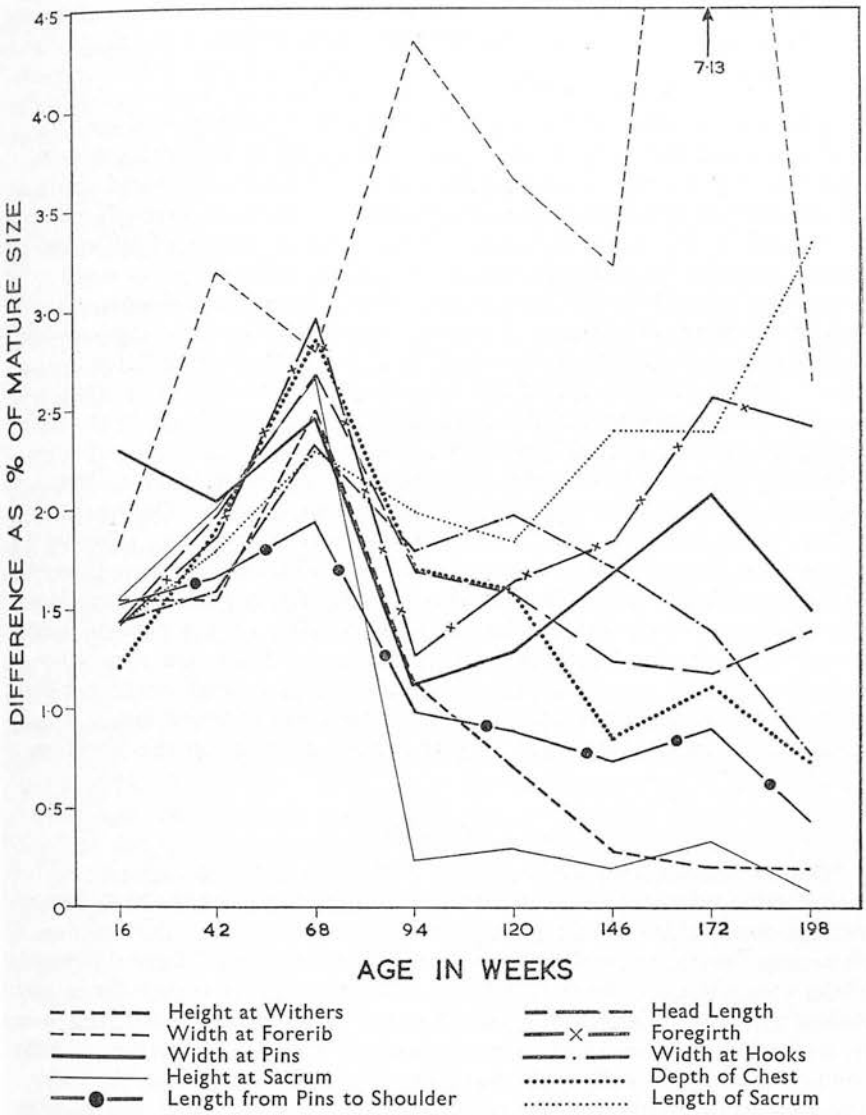

FIG. 2. Differences in growth for ten linear body dimensions at different ages, of twins split between 'high' and 'low' yielding herds. The differences at each age are expressed as percentages of mature size for each character.

The general pattern of Figure 2 is interesting in as much as it underlines differences between body parts. At the age of 16 weeks, the differences that had developed between the two treatment groups are fairly similar for all dimensions shown, but after that the lines of the graph begin to fan out—for some, e.g. heights at sacrum and withers, the differences have all but disappeared by 3 years old, for others, e.g. forerib width, foregirth or

sacrum length, the differences either continue at a high level or even increase. The differences when expressed as proportions of mean size at each age, confirm the impression from Figure 2 that the body conformation of the twins in the two groups is different—at 2 years old, for example, twins on *A* farms are broader and deeper animals than their co-twins on *B* farms, though apparently of much more nearly the same height.

Changes in classification of herds

The original classification of 130 herds into 2 yield groups was made, as stated at the beginning of this paper, on the basis of cow yields in a single year not long prior to placing out the calves. If herds are instead classified on the basis of cow yields over several years (6 years on average), ranking is reversed in four pairs of herds. Other methods of classification are of course possible, for example, the first lactation heifer yields averaged over a period of years. On this basis 5 herds would have changed sides. Again, instead of using an average of several years of heifer lactations, we may choose the year when the twins would be expected to be in milk for the first time. This is perhaps one of the most interesting lactations in relation to the growth of the twins and therefore in relation to the growth of the calves reared by farmers alongside the twins. It must be understood, of course, that many of the twins did not in fact survive long enough to have a lactation —though they would be reared with that lactation in view. On the criterion of this single lactation average, in the appropriate recording year (or the nearest year for which records were available), 13 herds which were originally classified as 'high' had, in fact, smaller heifer averages than their previously 'low' partners—a change of classification for 20% of the pairs of herds. Sample analyses for four body measurements and for five ages showed, however, that the general conclusions drawn in this paper would not have been altered by these re-classifications. Twins on the 'high' farms of each classification grew bigger on average than their co-twins on the 'low' farms.

DISCUSSION

One of the most interesting facts arising from this experiment is that the selection of two groups of commercial dairy farms on the basis of their average cow yields in a single year should have resulted in the selection of an average environmental or treatment difference which affects the growth of the young stock. Farmers did not know on what basis their farms were chosen and our evidence suggests that the twins placed with them were treated as other calves on the same farms. It is obvious, therefore, that the conditions for high milk yield went hand in hand with those for quicker growth—for the first 16 months of the animal's life at any rate. As was seen, the differences between the two groups in linear body measurements began to diminish, on average, after the age of 16 months. This is hardly surprising if we grant some measure of genetic control for the mature size of cows—as did Bonnier and Hansson (1946) and Bonnier, Hansson and Skjervold (1948), on the basis of their experiments with twins. Evidence on this point also comes from the study of Blackmore, McGilliard and Lush (1958) who have shown for single-born Holstein cattle that heritabilities for different linear body measurements increase with the age of the animals. The Swedish authors, using monozygous cattle twins split between two planes of nutrition, noted great growth differences between pairs and ascribed these

differences to genetical control. They also showed that the twins kept on a high plane of nutrition made more rapid early growth than their co-twins reared on a low plane. Hansson, Brännäng and Claesson (1953) on the basis of further experimentation again stress that 'rearing intensity has practically not influenced the size and proportion of the body at maturity' —though this is later elaborated, or perhaps rationalised, by the statement (Hansson, 1956) that 'the flexibility of the rate of growth decreases as the animal grows older' and that the rate depends at any stage on the level of nutrition employed earlier. The relevance of these Swedish experiments to our study lies not so much in any obvious similarities in design as in the apparently similar consequences on growth of our indeterminate treatment differences on the one hand and the precise nutritional differences of the Swedish work on the other.

In the present experiment, had the farmers in group *A* proceeded to treat their animals less well after they reached 16 months old than the farmers in group *B*—a situation which seems unlikely—then no doubt the accumulated growth differences could also have diminished as they did after 16 months.

The reading of Figure 2, showing the response of ten different body parts to treatment differences, was that body conformation is influenced by environment at all the eight ages shown (up to nearly four years old). The Swedish workers, already quoted, and Hammond (1948, 1949) have made similar findings. Hammond went so far as to suggest that what is called 'good conformation' within any breed depends to a large extent on the plane of nutrition on which the animal is reared. Underlying the veneer of environmental variation, however, there is a pattern of developmental stability, whereby each body part follows a pre-determined path from which it is deflected by the external environment only to a limited extent. This idea emerges in part from a significant degree of concordance for the rankings of the treatment differences for each of the 10 body parts at the eight ages (see Figure 2). Thus, while the ranking of these differences at any one age does not fully agree with that at the next, the concordance among all the ages is significantly high, the coefficient of concordance being 0·5 for all eight ages and 0·6 if the ranking at 16 weeks is excluded (see Kendall, 1948). More important evidence that each body part is following a line of development which is, to a considerable extent, independent of treatment comes from the correlation of the average ranking for each character (in order of differences) with the ranking of what Taylor (1958) has termed the growth potential of each body part. This growth potential measures the rate at which the various parts approach maturity. The correlation between such ranking worked out by Taylor for twins kept in a uniform environment and the present average order of differences is $\rho = 0{\cdot}8$ (significant at a 1% level). Hansson, Brännäng and Claesson (1953) came to similar conclusions regarding the behaviour of the different body parts.

It is rewarding that the results on growth from the present experiment, undertaken on commercial dairy farms, fall so well into the pattern revealed by more closely controlled experiments of different designs. In a further paper, it is hoped to report on the yield of the twins and on the relationship of growth and yield for the *A* and *B* farms. It is also proposed to analyse and report the nature of the treatment differences which, in their action, have produced the same effects as the nutritional differences of other experiments.

SUMMARY

Sixty-five pairs of two-egg cattle twins of three breeds, Ayrshire, Friesian, and Shorthorn, were split at random within a week of their birth between two groups of commercial dairy farms. One group was selected for a relatively high average milk yield of the adult dairy herd (group *A*) and the other for relatively low average yield (group *B*). The body growth of the twins up to nearly 4 years old is described in this paper. Very significant differences in growth developed in consequence of the split between the groups. Twins on the *A* farms became larger than their co-twins on the *B* farms. Average differences between the groups increased for the first year or 18 months and then began to fall away, but had not disappeared at the last age (198 weeks) studied. The various body parts behaved differently in response to the treatments or environments associated with the two groups of farms. Thus, at the ages studied, the twins on the 'high' yield farms differed in conformation from their co-twins on the 'low' yield farms. In addition to the differences arising between the members of split twin pairs, there were also differences in body size between the pairs. Breed was not apparently important as a factor affecting the growth differences arising between the two treatments.

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26

FACTORS INFLUENCING AVERAGE MILK YIELD OF HERDS AT TWO LEVELS OF PRODUCTION

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THE Animal Breeding Research Organisation started an experiment in 1950 to test the assumption that most of the differences in milk yield between herds of any one breed were due to management and other environmental factors. This assumption was partly based on early results from the use of bulls at artificial insemination centres in herds with very different levels of yield. These results showed that the genotypes of the bulls were of far less importance to the yield of their daughters than the level of production of the herd in which they were milked (Rendel and Robertson, personal communication). A further basis for the assumption arose from studies of breed structure (then in progress, though not published until later, e.g. Robertson and Asker, 1951; Wiener, 1953). These demonstrated that any genetic differences between herds, within a breed, would be rapidly disseminated through the population, (i) because most of the bulls used either came from a few studs or were direct descendants of such stud bulls, and (ii) because of continuous exchange of female stock between herds. Stated in another way, it was assumed that the genetic component of differences between average herd performance in milk yield was small. This thought, as well as being based on the reasons given, might equally well have followed from the practical observation that management can radically alter the level of milk production of any herd.

Drs. J. M. Rendel and A. Robertson were responsible for the experimental design. A number of dairy farms with high-yielding herds and an equal number with low-yielding herds were chosen on the basis of average milk production for mature cows. Purchased two-egg cattle twins were then split at random between the two yield groups. A comparison of the average yield differences shown by the twins on the one hand and the host herds on the other would indicate the importance of the environmental contribution to the average herd difference. One may assume that the twins split between the two groups represent, on average, two similar genetic samples. Therefore, should the average twin difference in yield be as great as that between the two groups of host herds, it would suggest that the yield difference between the two groups is due to environment only. Conversely, if the two groups of split twins yield the same, whilst the herds remain far apart, it would show that genetic differences were an important cause of yield differences between herds. The regression of twin differences on herd differences represents an estimate of the proportion of the total variation between herds which is due to environmental causes, and the remaining proportion represents variation due to genetic differences.

This paper presents the results on milk yield and discusses these in relation to management practices and to the differences in body size reported for the twins in this experiment (Wiener, 1959).

MATERIAL AND METHODS

Sixty-five pairs of female two-egg twins were purchased over the period from August 1950 to January 1954. The calves were of pure Ayrshire, Friesian, or Dairy Shorthorn breeding (though not necessarily of pedigree status). They were placed on farms in the West Midlands of England which carried milk recorded dairy herds of the same breed type. Each pair of twins was bought within a week of birth and immediately split at random between a farm having a relatively high-yielding herd and one having a lower-yielding herd. The average herd yields on which farms were chosen are based on cows in their second or subsequent lactation in a single milk recording year. This year was one or two seasons prior to placing out the twins. Table 1 gives the yield data appropriate to the year in which farms were probably selected.

TABLE 1

Average herd yields (cows only) at time of farm selection

		High		Low	
		Milk yield (lb./10)		Milk yield (lb./10)	
		Average	Range	Average	Range
Ayrshire	26	900	673-1,092	640	515-718
Friesian	24	1,100	803-1,314	700	563-897
Shorthorn	15	800	687-1,012	605	384-702

The slight overlap in yield shown between the ranges of the two groups within each breed type is due in every case to one herd only—the lowest yielder of the high group. Year-to-year variation in yield alters the situation represented by the ranges but the average differences remained distinct, though they became slightly less with the passage of years. All herds were to have a minimum of ten cows recorded, the average number was 23, with heifers in addition.

The twins were reared by farmers along with calves of their own. Our evidence suggests that, as intended, the twins were on the average treated in the same way as other cattle of similar age on the same farms. Each farm was given one twin only. Twins were weighed at 16 weeks old, and ten linear body measurements were taken also at 16 weeks old and at six-monthly intervals thereafter (for further details on measurements see Wiener, 1959). Twenty-four complete pairs survived to give a first lactation. This 24 is not far short of the number of complete pairs that would be expected to survive to complete a lactation if it is assumed that the chance of this is 2/3 for a single-born heifer calf (Milk Marketing Board, 1946/47). The nine pairs with complete second lactations bear no necessary relationship to the number that may actually have survived since the 'bargain' with co-operating farmers stipulated that, subject to ordinary husbandry considerations, twins need be kept through only one lactation—though a second was encouraged. Losses of twins were fairly equally divided between the two groups. Lactation records were obtained from the Bureau of Records of the Milk Marketing Board for the 24 surviving pairs of twins, and for all the herds participating in the experiment. There were a further 21 first lactations recorded from

heifers whose co-twin had not survived. Within breed, however, these lactations were divided so unequally between the high-yielding and low-yielding groups that they were not useful in analysis.

An attempt was made to obtain information on butterfat tests of the milk from twins and their contemporaries in the host herds—this met, however, with very little success.

There was considerable variation in age and season of calving between members of twin pairs; correction factors when applied are those given by Gilmore (1952).

RESULTS

Milk yield

The average first lactation yields of the twins and of contemporary heifers in the same herds are given in Table 2. This shows that in herds selected as high-yielding, the twins yielded about forty gallons less milk than their contemporaries, while in herds selected as low-yielding the twins produced

TABLE 2

First lactation milk yield (lb./10) of twins and contemporary heifers in high- and low-yielding herds

	High	Low	All
Twins	819	656	737
Contemporary heifers	859	646	752

ten gallons more. The average yield of the twins as a whole was fifteen gallons below the average of their single-born contemporaries, but this difference has no significance.

Table 3 shows the yield differences between the two groups of herds represented on the one hand by the twins and on the other by the average

TABLE 3

Differences in milk yield (lb./10) between high- and low-yielding herds

	No. pairs	Twins 1st lact.	Herd heifers 1st lact.	Herd cows 2nd and subsequent lact.	Twin diff. (heifer lact.) / Herd diff. (heifer lact.)	Twin diff. (mature equiv.) / Herd diff. (cows)
Ayrshire	10	176	157	227	1·12	0·97
Friesian	13	138	261	284	0·53	0·70
Shorthorn	1	353	143	69	2·47	5·65
All	24	163	213	251	0·77	0·86

yields of heifers and cows. Two pairs of herds (one pair Friesian, one pair Shorthorn) did not maintain their original 'high' and 'low' classification. For the purposes of Tables 2, 3 and 4 herds were re-classified according to average yield in the year that the twins lactated.

For Friesians the twin difference is less than the contemporary herd difference for heifers, whilst for Ayrshires (and for the single Shorthorn pair) the twins are less alike in yield than other heifers in the same herds.

Since there are more cows than heifers milking in these herds, differences based on average cow yields are less likely to be subject to random errors than differences based on heifer average. There is temptation, therefore, to adjust the first-lactation twin yields to a mature equivalent basis and then to compare these with the yields of the cows in the herds. The last column of Table 3 shows that this exercise has produced little change in the ratios of twin differences to herd differences. Moreover, the correction procedure may well be illegitimate since the factors used may not be applicable to our twin data.

Five pairs of Ayrshires and four of Friesians completed a second lactation. The Ayrshire twins differed by 250 gal. milk between high- and low-yielding herds whilst contemporary cow averages differed by 180 gal. For Friesians, the differences were 10 gal. for twins and 290 gal. for herds.

Calculations are based on yields up to 305 days only. In their first lactation, the twins in the high-yielding herds averaged one week longer

TABLE 4

Regressions of twin differences on herd differences

	No. pairs	b (1st lact.)	b (mature equiv.)
Ayrshire	10	1·17±·15	1·09±·22
Friesian	13	0·60±·26	0·60±·34
Shorthorn	1	2·47± —	5·66± —
All	24	0·76±·18	0·80±·22

in milk than their co-twins. This is unlikely to account for more than a small proportion of the yield difference between the two groups.

In order to give greater weight to the larger individual differences and in order to apply significance tests, a regression analysis was carried out. Results are shown in Table 4.

The regressions are estimates of the proportion of the total variation which can be ascribed to environment. Thus, on average, 76%±18% of the variation between herds in average milk yield of heifers is estimated as due to environment and the converse proportion, 24%±18%, to genetic differences.

The regressions do not differ significantly from unity. Differences between breeds are also not significant. The regression lines, however, do remove a significant part of the total variation in yield. In other words the evidence suggests that the whole of the yield differences between the herds could be due to environment but that if there is a genetic component, it is more likely to be between Friesian than between Ayrshire herds.

Age at calving

The twins entering the yield comparisons shown in Tables 3 and 4 calved over a considerable period but, on average, those in the high-yielding herds calved for the first time about seven weeks before the twins placed in the low-yielding herds. There was also considerable variation in month of calving. Since both age and month of calving are known to affect the level of milk yield, the question arises whether it is desirable to allow for these

variables in the yield differences between members of twin pairs. There is, however, no analogous information available for the herds into which the twins were placed—so that no correction could be applied to herd differences. It seems more prudent, therefore, to assume that, on average, the twin differences are representative of the herd differences and to apply no corrections for age at calving or for season. However, even when such correction factors were applied to twin differences in order to see what effect they would have on the regressions and their standard errors, shown in the preceding table, there was no significant change.

A comparison of age at first service and age at calving between high- (H) and low-yielding (L) herds is, however, of interest if the twins can be taken as representative of the herds in which they are reared. Table 5 gives information on twin pairs for which both members survived. In the top line

TABLE 5

Age at first service and calving (weeks) for two types of farm

Type of information available	No. of pairs	Age at 1st service		Age at 1st calving		Age at 2nd calving		Interval 1st serv.-1st calf		Interval 1st-2nd calving	
		H	L	H	L	H	L	H	L	H	L
1st service only	38	95·5	102·4	—	—	—	—	—	—	—	—
1st service and 1st calving	26	93·5	103·6	138·0	145·4	—	—	44·5	41·8	—	—
1st service, 1st calving and 2nd calving	14	85·1	105·2	129·8	146·0	184·3	197·7	43·7	40·8	54·5	51·7

data are presented for the maximum number of pairs of twins (38) with first service recorded, the second line gives data on the 26 pairs (included in the 38) which also have first calving recorded, and in the third line the information is confined to pairs with first service date and two recorded calvings.

It can be seen that twins in the high-yielding herd group were on average served earlier and calved earlier but that they did not apparently conceive as soon as their co-twins in the lower-yielding herds. Since at the age of first service the twins in the high-yielding group were on average bigger than their co-twins, it seems likely that farmers in both groups delayed first service until their animals had reached approximately the same body size. It appears from the last line of Table 5 that the twins in high-yielding herds also had a longer interval between first and second calving. However, for this group of 14 twins the total length of first lactation (not limited to 305 days) was on average two weeks longer for the higher-yielding members.

A larger proportion of the twins in the high-yielding herds calved in autumn, the time most favourable to total lactation yield, compared with their co-twins in the lower-yielding herd group. Thus, in any correction of the yield differences between the twins, the disadvantage of earlier calving in the high group is compensated by the advantage of calving at a more favourable time of year.

Effects of breed, year, and age on herd yield

Herds were classified according to the yield of cows as already explained. Average yields, separately for first lactation heifers and for cows, were followed through nine years for many of the sixty-five herds. Some interesting facts emerge. As might be expected, the average yield difference between the group classified as high and that as low diminished somewhat and a few herds switched sides (Wiener, 1959). This reduction in the average yield differences with the passage of years was of the order of 15% of the initial differences in heifer averages and 30% of those in cow averages. It occurred almost entirely through an improvement in the average yield of the low-yielding herds and not through deterioration of yield in the high group. Herds in the lower-yielding group were at a roughly similar yield

TABLE 6

Differences in yield for cows and heifers and breeds averaged over 9 *years* (1949-57) *for herds in two yield groups*

Breed	No. herds × years	Yield as % of Friesian				Heifer yield as % of cows		Ratio of cows : heifers contributing to herd average	
		High		Low					
		Cows	Heifers	Cows	Heifers	High	Low	High	Low
Friesian	152	100	100	100	100	82·1	83·5	2·2	2·5
Ayrshire	119	86·5	86·9	92·9	97·8	82·9	87·0	2·7	2·7
Shorthorn	63	75·6	71·7	90·8	90·5	78·5	82·4	2·1	2·5

level in all three breeds but more really high-yielding herds contributed to the Friesian high group than to the equivalent Ayrshire or Shorthorn group (Table 6). This could simply be a consequence of the availability of co-operating herds from the different breeds, but it might represent an expression of different breed potential for yield in two sets of environment. Differences between heifer yields and cow yields were greater in high-yielding herds than in low. In Table 6, data from several years are combined and expressed as percentages.

In Ayrshires in particular, but in the other two breeds also, the difference between heifer and cow yields is not the same in the two groups of herds. This might reflect a different age structure in the two types of herds—with fewer of the older cows at the peak of their milking ability in the lower-yielding herd group—but no information on age structure is available to test this explanation. However, one might suppose that such a difference would also be reflected in the ratio of cows to heifers contributing to the lactation herd averages. These ratios are shown in the last two columns of Table 6; they suggest, if anything, that more culling of cows takes place in the high-yielding herds, not the reverse. Herd size was similar in both types of herd (average number of lactations completed per year: Friesian 34 (H), 31 (L); Ayrshire 35 (H), 41 (L); Shorthorn 29 (H), 25 (L)).

Management and feeding

At each of the six-monthly visits to the twins, information was sought from the co-operating farmers on their management and feeding practice pertinent to the age group of animals with which the twin was associated. In most cases such information was readily given. Much of it could be verified from actual observation and some by comparing answers to similar questions at different times. This information is not specific to the twins but relates to the farms in general because it was the intention that the twins should be reared by the farmers along with their other stock and treated no differently. The field officers who collected these data are of the opinion that this intention was fulfilled in practice.

It is not proposed to detail in this paper the variety of farming practices met with in this experiment; the 130 farms involved appear to represent a cross-section of normal practices. It is intended merely to look for average differences between the two groups of farms—those selected for high- and those for low-yielding herds. Management differences, if they exist, may go some way towards explaining the differences in average herd production between the groups of farms and the average differences of the twins in respect of growth and yield.

(a) *Situation of farm.* The large majority of the farms were located in Cheshire and Staffordshire and the remainder in adjacent parts of Shropshire and Derbyshire. There was no average difference between the two yield groups in the elevation of the farms or in the type of land. A slightly larger proportion of the farms with high-yielding herds were thought to be situated in an exposed position than was the case for the other group (15% against 5%).

(b) *Housing and labour.* There was a great variety of housing both for young stock and milking cows. This ranged from the make-shift to highly specialised cattle accommodation, from dark, damp conditions to bright, well-ventilated ones. But in these descriptive terms it was not possible to arrive at an average assessment for the two groups. Instead, the impression formed from the detailed observations was translated into a more general assessment of whether the housing was good, or deficient in some way. Both at the calf stage and for older animals, the farms in the lower-yielding herd group came out slightly the worse on this average assessment—a larger proportion of them (about 10% more) being thought to provide less than good housing conditions for their stock.

The labour employed in looking after the stock was split according to family labour, hired workers, and sex. There was apparently no difference between the two types of farm in the proportion of men to women sharing the stock rearing. During the calf-rearing stage there was no difference in the extent of family participation in the work. But at subsequent stages of rearing and during the milking life of the cows, there was distinctly more family participation (about 20% more) on the high-yielding compared with the low-yielding farms.

(c) *Health and disposals.* Records were kept of the incidence of the more common ailments such as scour, ringworm and husk, of other illnesses both serious and mild, and of the extent of veterinary treatments and inoculations. For any one age it is not possible to say that one group differed from the other, but on balance over all ages there is a suggestion of less scour and husk

among the twins in the low-yielding herds, but slightly more of the 'other' illnesses. Twins in high-yielding herds had fractionally more veterinary attention and inoculations and came out slightly the better on a general assessment by the field officer of 'condition' of the twin when visited.

As already noted, many of the twins placed with farmers did not survive to complete a lactation. In an experiment such as this, relying on comparisons between members of twin pairs, the loss of one member disqualifies the pair as a whole. The important thing to know, therefore, in the comparison between the two groups of farms, is which was responsible for the loss of the first member of each twin pair. Table 7 shows the reasons for death or

TABLE 7

Causes of disposal of twins recorded according to the first member of each pair to be so affected

Cause of disposal	High-yielding farms	Low-yielding farms
Died as calf	2	1
Died at later stages but before 1st lactation	3	6
Disposal related to attestation scheme	3	3
Sterility	5*	7
Other hazards	7	4
Total	20	21

* Including one abortion.

disposal for the forty-one pairs where both twins did not complete at least one lactation.

The first thing to notice is that the two groups of farms contributed equally to the loss of intact twin pairs, and that there is no obvious difference within causes. Two of the calf deaths were due to scour and one to pneumonia; reasons for later deaths include accidents such as drowning, yew poisoning and bloat, as well as four unspecified deaths. Disposals related to the attestation scheme occurred because either the twin itself reacted to the tuberculin test in an attested herd (or in one entering the scheme), or because the herd as a whole was changed for new attested stock. The 'other hazards' include two cases where foot and mouth disease in the area led to the disposal of the whole herd, three cases where the farmer died or removed from the district and at least three cases where the farmer forgot the presence of the twin in his herd and sold it as surplus stock.

(d) *Feeding*. When visited at about sixteen weeks of age, the twins on the farms with high-yielding herds had received milk or milk substitutes for about a week longer, on average, than their co-twins, but the total quantity offered (94 gal.) was identical for both types of farm. The average estimated consumption of concentrates was similar; most of the farmers in both groups provided hay and there was no difference in the numbers who offered silage or roots. In both groups the calves were sent out to grass at an average age of seven months.

A few more (9 against 4) of the calves on the 'low' farms continued to

receive liquid feeding after the age of sixteen weeks than occurred on the 'high' farms, but in other respects there were no average differences in feeding noted for the six-month period up to forty-two weeks of age.

For the next six months there appear to be no further differences. Thereafter, from around eighteen months of age, there is evidence that more farmers in the high-yielding herd group were feeding concentrates—or at least recording the fact—and to animals of about two years old and over they were giving larger quantities. Unfortunately, too few twins survived, and even fewer farms with twins provided data on feeding, for firm conclusions about feeding to be drawn at these later ages and during the lactation period. Among such records as we have, there is, however, no suggestion of average differences between the groups in their feeding practices except for concentrates.

(e) *Breeding systems.* Eighty-eight per cent. of the high-yielding herds were either partly or wholly composed of pedigree cattle or cattle being graded-up to pedigree status. Among the low-yielding herds the equivalent percentage was seventy. All herds participating in the experiment were chosen, it will be recalled, for having a herd composed of pure-bred stock of predominantly one breed but without regard to pedigree status.

The same proportion (46%) in both yield groups used bulls from artificial insemination centres for some or all of their cows, but eighty-eight per cent. of the 'high' group and only seventy-four per cent. of the 'low' group kept their own bulls.

Body size and milk yield

It was established that twins in this experiment grew faster on the farms chosen for having high-yielding herds than they did on the farms with low-yielding herds. The body size differences, apparent at 16 weeks of age, increased up to the time the animals were about fifteen months old and thereafter declined slowly (Wiener, 1959). These findings gave, however, no clue of any relationship between the magnitude of body size differences and the magnitude of subsequent yield differences.

Estimates of linear regression of milk yield differences on body size differences were obtained. The data used for the yield differences were of two kinds (i) from the twins themselves and (ii) from heifer averages in the herds where twins were placed, but where these twins did not necessarily survive to complete a lactation. The year chosen for the heifer averages was that in which the twin in the herd lactated or would have done had it survived. Confining the information to the twins themselves has the advantage that the body size and yield data refer to the same animals. Using the herd data has the advantage that the relationships can be calculated for a much larger number of herds, but the disadvantage that the size information applies to only one representative in the herd.

Four representative body parts (head length, height at withers, length from pin bone to shoulder, and foregirth) were used separately to estimate regressions of milk yield difference on size difference. There was considerable sampling variation in the regression values both within and between ages. The overall pattern of the values suggests, however, a generally positive relationship with no obvious age trend.

A further step was to obtain a combined, weighted estimate of body

size using all ten body measurements on the twins at each age. This gave a measure of size less subject to error variation than individual body measurements. The size differences between the twins were then ranked and correlated with the correspondingly ranked yield differences—again using the two sources of milk yield data (heifer averages and twin yields). Yield differences based on heifer averages when correlated with the body size differences of the twins showed a predominantly positive relationship at later ages but a mainly negative relationship with size at 16 and 42 weeks old. The analysis was done in a stepwise fashion (all pairs represented at both 16 and 42 weeks of age; all pairs represented at both 42 and 68 weeks of age; etc.). Two estimates of correlation are therefore available for each age except the first (16 weeks) and the last (146 weeks). This stepwise analysis showed that in most cases the correlation increased from one age to the next.

TABLE 8

Estimates of rank correlations between body size of twins and average yield of heifers in the same herd—based on differences between high- and low-yielding herds

Age in weeks	Friesians	Ayrshires	Shorthorns	Average
16	−·14	−·40	−·36	−·32
42	−·11	·12	−·66	−·32
68	·03	·40	·24	·25
94	·38	·20	·22	·30
120	−·33	·27	·54	·02
146	−·01	·18	·70	·34

The two estimates of rank correlation for each age (except the first (16 weeks) and last (146 weeks)—see above) are based on slightly different, though overlapping, samples of twins and herds. The dual estimates were not always in good agreement with each other but since their differences, within age, are due to sampling only, the estimates have been pooled to produce Table 8.

The numbers on which the rank correlations are based vary: for Friesians between 14 and 16, for Ayrshires between 17 (at 16 weeks) and 9 (at 146 weeks); and for Shorthorns between 11 and 5 respectively. Although none of the individual correlations are significant, the separate estimates support each other to produce a fairly clear pattern.

When the rank correlations between differences in body size and differences in milk yield were restricted to the twins which themselves completed a lactation, the correlations tended, as before, to increase from one age to the next. They were also negative for early ages and positive for later ones. Since only one pair of twins of the Shorthorn breed completed a lactation, this breed does not enter the comparison.

The relationships presented here between body size at various ages and milk yield of heifers in their first lactation apply of course only to differences in body size which are greater or smaller than the average difference between the high- and low-yielding herds. Such an average difference was established in the previous study already referred to (Wiener, 1959). The new evidence suggests that at the calf rearing stage and up to about nine months old, larger

than average differences in body size were reflected by smaller than average yield differences. The reverse appears to be the case at later stages in growth and particularly at the age when twins were put in-calf, when a greater than average difference in body size was reflected by a greater than average difference in yield. These findings may well represent a difference between farmers with high-yielding herds and those with low-yielding herds in their approach to what represents the appropriate level of rearing of heifers for milk production.

DISCUSSION

A knowledge of the nature of differences in herd production is of practical importance because a majority of the farmers using natural service choose bulls largely on the reputation of the herds which breed the bulls. It is probable that many of these bull breeding herds are above average in milk yield, as for example the 'high' group in this experiment, but the relevant question is whether any part of this superiority is genetic. The numbers surviving in this experiment to the end of one lactation are too few for much reliance to be placed on the estimate ($\cdot 24 \pm \cdot 18$) of the genetic part of between-herd differences in heifer yield. However, the order of magnitude of the estimate is supported by estimates of other authors who quote figures ranging from less than 10% to about 25%—with the lower estimates strongly favoured (Robertson and Rendel, 1954; Robertson and McArthur, 1955; Pirchner and Lush, 1959).

Evidence of direct relevance to the findings of this experiment comes from one in New Zealand described by Brumby (1959). The two experiments have in common the use of twins split between high-yielding and low-yielding herds. On the basis of the performance of his one-egg twins and their contemporaries over two lactations, Brumby estimates that differences in milk yield between the herds were almost solely determined by environment and that about ten per cent. of the differences in fat yield were genetic in origin. Twins in the New Zealand trial were returned to the experiment station for a third lactation. This showed that the different levels of production of the twins whilst in high- and low-producing herds for two lactations had had little permanent effect on their subsequent production.

From these several sources of evidence, including the experiment described in this paper, the inference is that selection of breeding stock on the basis of average herd performance in milk yield is unlikely to represent much, if any, genetic selection. This is further reinforced by the findings that in Great Britain probably no more than a third of the total variation in milk yield (within breed and year) arises between herds and that the larger part (two-thirds or more) occurs between animals within herds (Robertson and Rendel, 1954—Friesians, Shorthorns, Guernseys; Wiener, 1957—Ayrshires).

None-the-less, actual differences in average herd production are large and undoubtedly important in economic terms. Hence the attempt to study the management of the herds in the two yield groups in this experiment, particularly as the farms of both groups represent dairy farms in a part of England where dairying is important.

As mentioned earlier, the farms in this experiment displayed a wide range of variations on management practices. Average differences between the two groups were not very obvious. Perhaps the greater personal participation

in the stock management on the part of the farmers with high-yielding herds, and the slightly larger proportion of these herds with pedigree stock are significant signs. But it is most unlikely that a difference of 12% in the number of farms having some animals of pedigree status would in itself play an appreciable part in the yield difference between the two groups (Milk Marketing Board, 1957). In the Ayrshire breed, grading-up to pedigree status is associated with selection for milk yield (Wiener, 1957), but an equal number of Ayrshire herds in both our yield groups participated in this scheme.

There appears to be no obvious difference in feeding practice, certainly of younger stock, in the two groups. This, however, is a quantitative assessment which takes no account of possible differences in the quality of feeding stuffs and pasture. Some difference, either in nutrient intake through better quality food, or in efficiency of utilisation through better management, seems indicated by the quicker growth of the twins on the high farms. Information on animals older than eighteen months is meagre in this survey, but it gives a hint that more concentrates were fed from that age onwards to twins in the high-yielding herds than were given to co-twins in the other group. This hint supports the stress generally laid by nutritionists on adequate feeding a little prior to and during lactation. The evidence for a relationship between differences in body size and differences in milk yield lends some indirect support here, particularly the small but positive correlation at eighteen months to two years of age.

An interesting difference between the two groups is the magnitude of the increase in average milk yield between heifers and cows. The average increase is from one-and-a-half times to two times as great in the high-yielding herds as it is in the low-yielding ones. This, also, was a feature of the differences between the two groups of herds in the New Zealand experiment, already quoted (Brumby, 1959). Since cows do not reach peak production for several lactations, one might assume that high-yielding herds have a larger proportion of older cows. This has been found to be the case in the New Zealand study. In our experiment, the proportion of heifers was in fact greater in the low-yielding group. An explanation which would fit the facts, but which we cannot test, is that in high-yielding herds heifers, and cows, are more stringently culled for poor production than in lower-yielding herds. Alternatively, the greater potential for milk production after the first lactation may be realised more fully under the environmental conditions of the high-yielding herds than under those of the low-yielding herds.

In the absence of information on milking techniques and feeding during lactation, several questions must be left untouched. However, from the reported differences in growth rates of the twins, it is obvious that management differences must have existed between the groups from the first. It is unlikely, however, that differences in rearing of calves and of young stock would account for more than a fraction of the yield differences. Otherwise, even with our small numbers, one would have expected a far stronger relationship between body size differences and yield differences than have been found at any age.

Consulting officers of the New Zealand Dairy Board who studied the limiting factors to high production on 118 low-producing dairy farms concluded that the standard of feeding of the herd was the main factor (N.Z. Dairy Bd., 1955). Their report further suggests that the managerial ability

of the farmers determined the level and efficiency of farm production. Scott and Phillips (1959) have reported on the management practices of the high-yielding and low-yielding herds of the experiment in New Zealand analogous to that described in this paper. There are a number of points of contact between the two experiments in the factors chosen for study and there is some agreement in the respective findings despite differences in farming systems between the two countries. Above all, however, there appears to be agreement that no single factor of management or environment could be pointed to as the cause of the differences in production between the herds.

SUMMARY

An experiment was started in 1950 designed to find out what proportion of the difference in milk yield between herds is genetic in origin. Sixty-five pairs of twins were split at birth equally between farms having high-yielding herds and farms having low-yielding herds. A previous paper on this experiment reported on the growth of the twins, the present paper on milk yield and on management practices in the herds.

Twenty-four pairs of twins survived to complete one lactation and these provide an estimate of 24%±18% for the genetic part of the difference between the herds.

Aspects of rearing of the twins and of management of the herds were examined. Twins in the high-yielding herds were served and calved earlier than those in the low-yielding group but they had a longer interval between service and calving. Differences between average heifer yields and average cow yields were from one-and-a-half to two times greater in the high- than in the low-yielding herd group. There were no obvious quantitative differences in feeding practice between the two groups although differences in body size suggest that twins in the high group were done better. For the age at first service there was a positive rank correlation of 0·30 between body size differences and subsequent differences in first lactation milk yield. There was no single factor of management or environment which appeared to be the cause of the yield difference between the herds.

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The Size of Lambs at Birth—A Study Involving Egg Transfer

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THE SIZE OF LAMBS AT BIRTH—A STUDY INVOLVING EGG TRANSFER

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THIS paper describes two experiments involving the transfer of fertilised sheep ova (1) from Lincoln to Welsh Mountain ewes and vice versa, and (2) from Lincoln and from Welsh Mountain ewes to Blackface ewes. The paper is concerned with birth data on the lambs and some associations with parental size.

An early demonstration of the importance of maternal influence on the size of offspring was provided by the reciprocal cross between Shire horse and Shetland pony (Walton and Hammond, 1938). The most noteworthy features of that experiment arose from the large difference in parental body size. Reciprocal crosses in cattle between the South Devon and Dexter breeds (Joubert and Hammond, 1958) and in sheep breeds between Border Leicester and Welsh Mountain (Hunter, 1956) and Lincoln and Welsh Mountain (Dickinson, Taylor and Wiener, unpublished) have also utilised large differences in parental size to demonstrate maternal effects. In general, such studies have shown that differences in the size of the young at birth are related to their mother's size to a varying extent. Interpretation of the results from these reciprocal crosses, however, has relied heavily on the assumption that the crossbred offspring from the two types of mother are genetically identical—yet, largely on account of small numbers, the gene sample contributed by males and females of the same breed may not be equivalent.

In the study of mother-offspring relationships the transfer of eggs between breeds has many advantages over reciprocal crossing. It makes possible (i) maximum maternal/foetal size ratios, (ii) novel maternal-foetal combinations, (iii) direct comparisons of maternal environments within sires, (iv) direct estimation of genetic and maternal covariation, (v) control of the number of offspring—an important matter when multiple births would occur naturally. Venge (1950) first used the technique of egg transfer to study maternal-foetal relationships in rabbits, Brumby (1960) used the technique in mice, and Hunter (1956) had birth data on egg transfers in his experiments with sheep.

For convenience, we shall refer to the mother's role in affecting the growth of the embryo as the effect of the *maternal environment* though it is obvious that this is in part conditioned by her genotype. Similarly, the embryo's growth will be referred to in terms of the *lamb's genotype* although it is equally clear that there are likely to be interactions between the embryo's growth and its mother's physiological processes.

MATERIAL AND METHODS

The surgical technique used in the egg transfer was that developed by Hunter, Adams and Rowson (1955). Modifications of procedure used here

have been described elsewhere (Hancock and Hovell, 1961) or are specified below.

Experiment 1. Matings and operations took place in the autumn of 1959: lambs were born in the spring of 1960. The breeds of sheep used were pure Lincoln and pure Welsh Mountain. The ewes of both breeds were born in their native regions but were reared from the age of 6 months (in 1955) on the Animal Breeding Research Organisation's farm in Peebles-shire—a good, semi-upland grass farm. Reciprocal transfers of fertilised eggs were made between the two breeds. The recipient ewes were 4½ years old and had already had three previous lamb crops by normal means (i.e. not transferred). The same applies to the donors with the exception of 3 nulliparous Lincoln females, which were 18 months old. Females surplus to requirements as donors and three which had already served as donors

TABLE 1

Design and numbers for Experiment 1

Breed of ewe	Lincoln		Welsh	
Breed of lamb	Lincoln (N)	Welsh (T)	Lincoln (T)	Welsh (N)
No. of donors	—	6	9	—
No. of lambs born				
single	6	7	13	8
twin	8	2	—	12

N = born in the normal way. T = born from transferred eggs.

were subsequently mated to produce lambs by normal means. Such lambs were inevitably born later, on average, than those in the transfer groups. Only one Lincoln ram was used and all but two of the Welsh lambs were sired by the same Welsh ram. Seven of 13 Lincoln ewes with Welsh eggs and 13 of 20 Welsh ewes with Lincoln eggs gave birth to single lambs. In addition one Lincoln ewe had Welsh twins. Details of numbers are given in Table 1. Up to four transferred offspring were born per donor.

Experiment 2. Eggs were obtained in the autumn of 1960 from old Lincoln and old Welsh ewes and transferred into 1½-year-old nulliparous Scottish Blackface females (gimmers). In other words, eggs from two breeds of donor were transferred to one breed of recipient. Synchronisation of heats of donor and recipient was achieved either by selecting (from a flock of 200) Blackface females with heats spontaneously synchronous with those of potential Lincoln and Welsh donors, or by regulating the onset of heat in the donors by treatment with progesterone followed by PMS. Most of the Lincoln ewes were the same as those used in the previous year; the Welsh ewes were derived from the same hill flock in Wales as those used before but had been reared on the hill throughout their life. One Lincoln and one Welsh ram were used. Lambs, all singles, were born in the spring of 1961. Thirty-six of 41 recipients of Lincoln eggs and 28 of 37 recipients of Welsh eggs gave birth to lambs. Details of numbers are given in Table 2. Up to six transferred offspring were born per donor.

MANAGEMENT

Experiment 1. Subsequent to the transfer operations the sheep in Experiment 1 were moved to the semi-upland farm where they outwintered at grass but received supplements from the end of January. Hay was given for about 5 weeks and a mixture of bruised oats and ewe nuts (3 : 1) for about 14 weeks.

At lambing the Lincoln and Welsh ewes were run with a larger flock of ewes of several breeds and were given only normal supervision as a part of this larger flock, which was visited early in the morning and again at dusk. The sheep ran at grass throughout lambing. Among the ewes carrying lambs to full term no difficulties were experienced with the Lincoln ewes but among the 13 Welsh ewes carrying Lincoln lambs, 8 were assisted at parturition. Two of the assisted cases involved partly born lambs discovered in the morning and found to be dead due to asphyxia. Both lambs were males and, when removed from their mothers, weighed 14·0 and 12·4 lb.; their Welsh dams remained weak for a day or two but then recovered. In the non-transfer group, 2 Welsh lambs were found dead (cause unknown) at birth but normally delivered.

TABLE 2

Design and numbers for Experiment 2

Breed of ewe (recipient)	Blackface	
Breed of lamb	Lincoln	Welsh
No. of donors	15	12
No. of lambs born (single)	35†	28

† = excluding one born approximately 3 weeks premature.

Experiment 2. The Blackface gimmers of Experiment 2 remained at the Field Station where the operations had been performed but, owing to an insufficiency of grass, were fed hay estimated at 1 lb. per head/day and concentrates in the form of ewe and lamb nuts rising to a maximum of 1 lb. per head/day. Shepherding was no more than normal for a flock at grass.

During lambing time, the Blackface gimmers carrying Lincoln lambs were run separately from those with Welsh lambs and while the former were closely watched and veterinary supervision was available, the latter group was visited only twice a day and only one Welsh lamb was assisted into the outside world. It is possible therefore that among Blackface gimmers with Lincoln lambs some which were assisted might have been left to their own devices under the conditions obtaining for Experiment 1. Sixteen of the 36 Lincoln lambs were assisted; one, a male weighing 14·8 lb. was stillborn; all others were born alive. All presentations were normal. The indications for interference were prolonged second stage labour with gimmers becoming exhausted and the consequent fear that lambs might die before parturition was completed. Assistance took only the form of traction.

RECORDING OF DATA

Measurements of lambs were made within 12 hours of birth. Cannon length was measured, to the nearest millimetre, externally on the fully flexed fore-limb. Weights were taken to the nearest tenth of a pound.

Gestation length was recorded to the nearest half day commencing from the time of mating, taken in the case of transferred lambs as the time of mating of donors (which, except in 3 cases, was the same as the time of sterile mating of recipients).

RESULTS

Comparisons of mean size

Experiment 1. Table 3 presents mean values for the characteristics of single-born lambs and their mothers. Four Lincoln and 6 Welsh ewes in the normal group and one Lincoln ewe in the transfer group had twins all of which we excluded from the analysis.

TABLE 3

Characteristics of single lambs and their mothers (*Experiment* 1)

Breed of dam (4th parity)	Lincoln				Welsh			
Breed of lamb	Lincoln		Welsh		Lincoln		Welsh	
Sex	♂	♀	♂	♀	♂	♀	♂	♀
Number of lambs	3	3	4	3	4†	9	3‡	5
Donor's wt. (29.9.59) (lb.)§	188·3	227·3	111·5	108·3	195·5‖	186·7‖	116·7	105·2
Recipient's wt. (27.1.60) (lb.)§	163·0	198·3	179·0	168·0	101·3	91·8	94·3	87·2
Av. date of birth (days from 1st Jan.)	134	158	114	113	112	101	140	137
Birth weight (lb.)	16·0	13·9	10·0	8·5	13·0	11·5	8·9	8·0
Cannon length (cm.)	10·8	10·1	8·7	8·1	10·4	9·9	8·6	8·0
Gestation length (days)	148·0	146·3	151·0	151·7	147·5	147·7	148·0	146·4

† including 2 that died during parturition.
‡ including 1 stillborn.
§ in the non-transferred group the weights refer to the same ewes at the two different dates.
‖ excluding the weights of the three 18-month-old females used as donors.

The extent to which the experimental methods have achieved randomisation can be assessed from the mean dates of birth and the mean weights of donor and recipient ewes within sub-groups. There was an average difference of 3–6 weeks in the date of birth between transferred and normal lambs. This was largely inevitable for the reasons given earlier, but the effect of this difference is to introduce a bias of unknown magnitude into some of the comparisons. Within transfer and normal groups randomisation has been reasonably satisfactory in respect of mean date of birth. As far as weights of donors are concerned those that provided eggs for transfer were not significantly different from those which went on to produce lambs in the normal way—and the same is true for recipients.

As seen from Table 3, male lambs were on average consistently heavier at birth and had longer cannons than female lambs. While not all these differences were statistically significant within sub-groups, the average sex difference over all groups was highly significant ($P<0{\cdot}001$). For both Lincoln and Welsh lambs, females were close to 86% of average male birth weight

in the Lincoln maternal environment, but close to 89% in the Welsh maternal environment. For gestation length the sex difference went in opposite directions in the normal and transfer groups and the average difference of 0·61 days was not significant.

Comparisons involving the size of lambs at birth and their gestation length are now presented in terms of differences due to maternal environment and to genotype of lambs. Lambs of the same breed differed in birth weight according to whether their uterine environment was Lincoln or Welsh. Lambs reared in the same uterine environment differed in birth weight according to whether their genotype was Lincoln or Welsh. The magnitude of these differences in birth weight together with the corresponding differences in cannon length and gestation length are given in Table 4.

Individual entries may be biased (whether up or down is not known) as a consequence of the difference in average lambing date of normal and transferred lambs. The assessment of whether the lamb's genotype or the influence of the maternal environment is the greater is, however, unbiased, as is the effect of genotype averaged over Lincoln and Welsh maternal environments, and the effect of maternal environment averaged over the two lamb genotypes.

Both genotype of lamb and maternal environment have a significant influence on the birth weight of the lambs. In all four comparisons the maternal influence is much less than the genotypic influence. If the total difference between normal Lincoln and normal Welsh lambs is broken down into an average effect of lamb's genotype and an average effect of maternal environment, only 24% of the total difference in birth weight is due to maternal environment in the case of female lambs and 29% in the case of male lambs. However, these average effects do not fully describe the situation. There is probably an interaction between the genotype of the lamb and its maternal environment. Lambs with a Lincoln genotype appear to be much more affected by the different maternal environments than are lambs with a Welsh genotype. Also, the difference due to the lamb's genotype is more pronounced in the Lincoln maternal environment than in the Welsh maternal environment. In the Lincoln maternal environment, Lincoln lambs were on average 22% heavier but Welsh lambs only 9% heavier than in the Welsh maternal environment. These percentages differ significantly ($P<0·01$) but three biases have to be considered. The first, due to differences in date of lambing, would tend to increase the difference between the percentages if late born lambs are lighter and decrease the difference if the effect is in the opposite direction. Which, if either, direction would apply in this case is unpredictable. The second bias is that the number of lambs born to a ewe has been controlled only in the case of the transfer groups. Singles thus enforced on ewes which might under natural circumstances have had twins are, if anything, likely to be heavier than naturally occurring singles. Any allowance for such an effect would increase the interaction; that is, the normal Lincoln lambs would be even more than 22% heavier than the transferred Lincoln lambs whereas Welsh lambs out of Lincoln mothers would be closer to the weight of normal Welsh lambs than the 9% found. The third bias arises from the fact that lambs born to their own breed of mother were not subjected to randomised transfer.

The results for cannon length at birth are of a similar nature, but different in magnitude. The influence of maternal environment is small and mainly

insignificant; in this particular situation the genotype of the lambs would appear to have dominant control of cannon length at birth. Of the total difference between normal Lincoln and normal Welsh lambs, only 9% is due on average to maternal environment in the case of female lambs, and 13% in the case of male lambs.

TABLE 4

Differences (and standard errors) in birth weight, cannon length and gestation length between transferred and normal Lincoln and Welsh lambs (Experiment 1)

(*a*) Effect of maternal environment (Lincoln—Welsh)

Genotype of lamb	Sex of lamb	Effect of maternal environment on: Birth weight (lb.)	Cannon length (cm.)	Gestation length (days)
Lincoln	♀	2·4±1·0	0·20±0·21	−1·3±1·4
	♂	3·1±0·7	0·45±0·08	0·5±1·2
Welsh	♀	0·4±0·4	0·17±0·24	5·3±1·3
	♂	1·1±0·7	0·15±0·26	3·0±1·4
Average	♀	1·4±0·6	0·19±0·16	2·0±0·9
	♂	2·1±0·5	0·30±0·16	1·8±1·0

(*b*) Effect of lamb's genotype (Lincoln—Welsh)

Maternal environment	Sex of lamb	Effect of lamb's genotype on: Birth weight (lb.)	Cannon length (cm.)	Gestation length (days)
Lincoln	♀	5·4±1·1	1·97±0·07	−5·3±1·4
	♂	6·1±1·0	2·08±0·35	−3·0±1·5
Welsh	♀	3·5±0·8	1·94±0·20	1·3±1·0
	♂	4·1±0·3	1·78±0·19	−0·5±0·6
Average	♀	4·5±0·6	1·96±0·16	−2·0±0·9
	♂	5·1±0·5	1·93±0·16	−1·8±1·0

(*c*) Interactions between lamb's genotype and maternal environment

Sex of lamb	Effect of interactions on: Birth weight (lb.)	Cannon length (cm.)	Gestation length (days)
♀	1·0±0·6	0·02±0·16	−3·3±0·9
♂	1·0±0·5	0·15±0·16	−1·3±1·0
Average	1·0±0·4	0·08±0·11	−2·3±0·7

The results for gestation length differ in type from those for lamb's size. The average effect of the Lincoln maternal environment is to give significantly longer gestation length by about 2 days than is given by the Welsh maternal environment. The average effect of the lamb's genotype turned out to be equal and opposite to the average effect of the maternal

environment. In both cases there appears to be a strong interaction. In fact, normal Lincolns, normal Welsh, and Lincolns transferred into Welsh all appeared to have about the same gestation length, but the Lincoln maternal environment significantly prolonged the gestation length of transferred Welsh lambs, both male and female, by about 4 days. The result, stated in this way, however, is now subject to the bias due to the differences in date of lambing of normal and transfer lambs. Terrill and Hazel (1947) have found that the later in the season lambs are born, the shorter their gestation length. An allowance for this would tend to remove the interaction and lead to the conclusion that Lincoln lambs transplanted into Welsh mothers had a shorter gestation length than normal Welsh lambs, and that Welsh lambs transplanted into Lincoln mothers would still be carried longer than normal Lincoln lambs but not by as much as suggested above.

Experiment 2. The results are given in Table 5. Donors' and recipients' weights and their lambing dates are presented as before as a check on the randomisation achieved. Recipient ewes' weights are satisfactorily alike in the different sub-groups and, for date of lambing, no two subgroups differ by more than one day. Correlations of donor's weight with recipient's weight were all found to be negligible.

TABLE 5

Mean characteristics of the lambs (singles) and their mothers (Experiment 2)

Breed of dam (1st parity)	Blackface			
Breed of lamb	Lincoln		Welsh	
Sex	♂	♀	♂	♀
Number of lambs	17	18	16	12
Donor's weight (lb.)	187·5	197·8	72·1	71·4
Recipient's weight on 30.1.61 (lb.)	106·4	111·9	103·6	101·1
Av. date of birth (days from 1st Jan.)	93	93	94	93
Birth weight (lb.)	10·8	9·7	7·6	6·9
Cannon length at birth (cm.)	10·1	9·7	8·5	8·2
Gestation length (days)	147·2	146·2	147·8	146·6

There was a significant sex difference at birth both in the mean weight and mean cannon length of lambs. Females were 90% of the weight of males both for Lincoln and for Welsh lambs; and the corresponding figure for cannon length was 96·6%. There was also a significant average sex difference of one day in gestation length, males being carried longer than females. This is the case in many mammalian species (McKeown and MacMahon, 1953) but has not generally been found in previous work with sheep (Terrill and Hazel, 1947).

The main result of experiment 2 is that in the Blackface maternal environment Lincoln lambs were at birth clearly and very significantly larger than Welsh lambs by $3·2 \pm 0·5$ lb. for males and $2·7 \pm 0·5$ lb. for females in liveweight, and by $1·58 \pm 0·13$ cm. for males and $1·46 \pm 0·17$ cm. for females

in cannon length. Lincoln lambs had a gestation length half a day shorter on average ($0{\cdot}6 \pm 0{\cdot}5$ days for males and $0{\cdot}4 \pm 0{\cdot}7$ days for females) than Welsh lambs but sampling errors readily account for this half-day difference.

Variation in size at birth

Partition of variation in group means. Components of variance were computed from the mean values for each lamb characteristic in both experiments (Table 6). Lamb's genotype accounts for 72% of the variation in birth weight and 97% of that in cannon length; maternal environment is responsible for 20% and 1% respectively. These figures show clearly that mean cannon length is subject to greater genetic control than is mean birth weight. The large genetic difference in mean size between the Lincoln and Welsh breeds dominates the situation to such an extent in the case of cannon

TABLE 6

Partition of total variation in group means (sexes averaged)

Component of variance	Percentage of total variance		
	Birth weight	Cannon length	Gestation length
Lamb's genotype	72	97	0
Maternal environment	20	1	0
Maternal-foetal interactions	7	1	86
Error	1	1	14
Total variance	11·7 (lb.)^2	1·7 (cm.)^2	3·8 (days)^2

length that the maternal and interaction components appear trivial. Nevertheless they are significant effects responsible for a range of about half a centimetre in cannon length. In the case of gestation length all variation went into interaction and error.

Comparisons of variation within groups. The average coefficient of variation for birth weight was 12% and for cannon length 4%. In their normal maternal environment, however, the variation shown by Welsh

TABLE 7

Variances within group and sex

Maternal environment	Degrees of freedom		Birth weight (lb.)^2		Cannon length (cm.)^2		Gestation length (days)^2	
	Lincoln lamb	Welsh lamb	Lincoln lamb	Welsh lamb	Lincoln lamb	Welsh lamb	Lincoln lamb	Welsh lamb
Lincoln (4th crop)	6	7	0·53	0·50	0·02	0·09	2·8	2·1
Welsh (4th crop)	13	8	2·02	0·18	0·08	0·09	1·9	3·2
Blackface (1st crop)	33	26	2·71	0·45	0·20	0·12	3·0	2·0

lambs did not differ significantly from that shown by transferred Welsh lambs in either weight or cannon length at birth (Table 7). For Lincoln lambs, on the other hand, the effect of transfer into the probably restricting Welsh maternal environment was to bring about a significant four-fold increase in variance. When Lincoln lambs were transferred into the even poorer maternal environment (as judged by birth weight) provided by the first parity Blackfaces, the variance showed an even greater increase, five-fold for birth weight and ten-fold for cannon length. This comparison is, of course, partially confounded with a year difference, yet for gestation length the variance was very similar in all six sub-groups, the overall average variance within subgroups being 2·55 (days)^2 with 32 d.f. in Experiment 1 and 2·63 (days)^2 with 59 d.f. in Experiment 2.

Inter-relationships of lamb size and weight of donor and recipient. As a consequence of the randomised transfer of eggs from donor to recipient, the covariation between donor ewe and lamb can be defined as genetic while that between recipient ewe and lamb can be defined as maternal.

TABLE 8

Correlations between lamb's size and maternal size

	Donor's weight				Recipient's weight			
	L♂	L♀	W♂	W♀	L♂	L♀	W♂	W♀
Birth weight	0·41	−0·12	−0·05	0·13	0·57	0·33	0·23	0·26
Cannon length	0·45	0·39	−0·16	0·24	0·55	0·13	0·43	0·15

The number of lambs available in Experiment 2 within sexes and breeds of lamb are sufficient to yield useful information on the relationships between weight and cannon length of lamb and weight of donor ewe (just prior to mating) and of recipient ewe (8 weeks before lambing). Correlations are shown in Table 8.

The correlations of birth weight with donor's weight were small and insignificant (average $r = 0·09$) and it follows from this that donor's mature weight gave next to no indication of her lamb's weight at birth. Donor's weight accounted on average for only 1% of the total variation in birth weight of the lambs. The correlations with recipient's weight were considerably higher (average $r = 0·35$) but even so accounted on average for only 14% of the total variation.

For cannon length, the correlations with donor (av. $r = 0·23$) were again less than those with recipient (av. $r = 0·31$) but by only a small margin. Donor's weight and recipient's weight each accounted for only about 7% of the variation in cannon bone length.

The covariances of lamb's size at birth with donor's (mature) weight are direct genetic covariances. The minimum genetic correlation of lamb's size with its *own* mature weight can be obtained by the conventional method of doubling the donor-lamb correlations, and so incorporating the genetic contribution of the sire. Selection for ewe's mature weight would apparently be more efficiently carried out by selection at birth on cannon length (average correlation = 0·46) than on weight (average correlation = 0·18). These actual values, however, may change in other environmental situations. As

it is, the correlations tend to be lower, though not significantly, for Welsh lambs than for Lincolns and if the higher correlations for Lincoln lambs are a consequence of their more restricted prenatal growth, then this result would agree with that found for birth weight in cattle (Dickinson, 1960), where predictability was higher in the more restrictive maternal environment.

Although very little of the variation in lamb's size has been accounted for by donor's or by recipient's weight, many of the regressions are nevertheless far from negligible. In relative magnitude they repeat the trends of the correlations. For birth weight, the regression of lamb on recipient ($0{\cdot}043 \pm 0{\cdot}014$ lb./lb.) is much greater than that on donor ($0{\cdot}008 \pm 0{\cdot}009$ lb./lb.) while for cannon length the regressions are more nearly equal ($0{\cdot}010 \pm 0{\cdot}005$ cm. for each lb. increase of recipient's weight and $0{\cdot}007 \pm 0{\cdot}003$ cm. for each lb. increase in donor's weight). Although in no case was there significant heterogeneity among breeds or sexes, the regression of birth

TABLE 9

Within- and between-group regressions of lamb size on recipient ewe's weight

Lamb	Birth weight (lb./lb.)		Cannon length (cm./lb.)	
	Within (Blackface recipients)	Between breed means	Within (Blackface recipients)	Between breed means
Lincoln ♂	$0{\cdot}096 \pm 0{\cdot}03$	$0{\cdot}066 \pm 0{\cdot}117$	$0{\cdot}015 \pm 0{\cdot}006$	$0{\cdot}009 \pm 0{\cdot}004$
♀	$0{\cdot}046 \pm 0{\cdot}03$	$0{\cdot}031 \pm 0{\cdot}022$	$0{\cdot}007 \pm 0{\cdot}014$	$0{\cdot}003 \pm 0{\cdot}003$
Welsh ♂	$0{\cdot}014 \pm 0{\cdot}02$	$0{\cdot}020 \pm 0{\cdot}016$	$0{\cdot}020 \pm 0{\cdot}012$	$0{\cdot}002 \pm 0{\cdot}001$
♀	$0{\cdot}012 \pm 0{\cdot}01$	$0{\cdot}012 \pm 0{\cdot}015$	$0{\cdot}002 \pm 0{\cdot}005$	$0{\cdot}001 \pm 0{\cdot}001$

weight on recipient's weight was more than five times as great for Lincoln lambs as for Welsh lambs.

The regressions found within subgroups can be compared with regressions derived from group means for maternal size and lamb size as given by the experiments in both years. Of the variation in birth weight due to maternal environment as defined by breed type, 60% is accounted for by linear regression on recipient's mean weight and for cannon length this is 82%. The between-breed regressions and the within-group regressions are in considerable agreement for the regression of birth weight on recipient's weight (Table 9). This suggests that the maternal environment is reasonably well defined by recipient's weight whether derived from individuals within groups or from breed mean weights. Figure 1 illustrates the relationship of lamb size to recipient size for the different foetal types and, because the lines diverge, shows that the genotype-environment interactions, far from being haphazard, are part of a regular pattern.

In the case of donor's weight, the within-group regressions tended to be less than the between-group regressions even when allowance is made for the sires' contribution. In the Blackface maternal environment, the average regression of birth weight on donor's weight from within-group analysis was $0{\cdot}008 \pm 0{\cdot}009$ lb./lb. which, if doubled to allow for the sires' contribution, is to be compared with the between-breed figure of 0·035 lb./lb. Their ratio provides a tentative estimate of 0·46 for the heritability of mature

weight. In the Lincoln and Welsh maternal environments, however, the between-group regressions were higher (0·068 lb./lb. and 0·045 lb./lb. respectively). For cannon length the average within-group regression was 0·007±0·003 cm./lb. and, if doubled as before, is to be compared with the regressions derived from breed mean size of 0·018 cm./lb. in Blackface mothers (0·024 cm./lb. in Lincoln mothers, and 0·022 cm./lb. in Welsh mothers). The ratio again estimates the heritability of mature weight, in this case as 0·77.

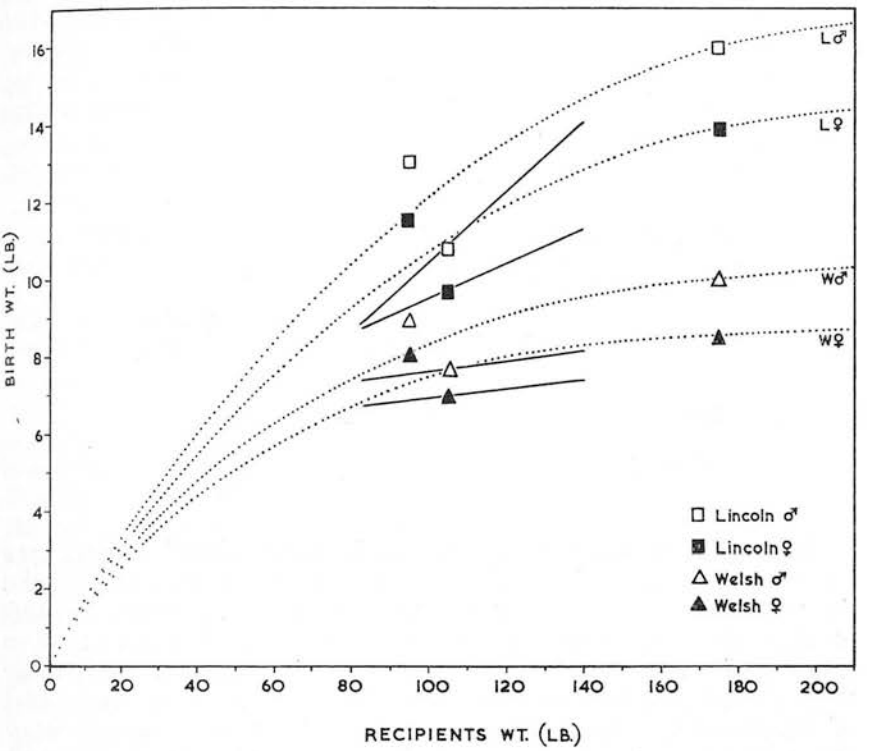

FIG. 1. The relationship of birth weight to recipient ewe's weight as shown by the group means from experiments 1 and 2, by the regression lines calculated for Blackface mothers, and by a hypothetical curve for each of the four genetic types of lamb over the full range of maternal environments.

Relationship of birth weight and cannon length. In Blackface mothers, the association between the birth weight of a lamb and its cannon length is seen to be strong and is stronger for Lincoln lambs than for Welsh lambs (Table 10, col. 1). To what extent is this association genetic and to what extent is it induced by the maternal environment provided by the recipient ewe? The partial correlations of birth weight and cannon length, with recipient ewe's weight held constant, scarcely differ from the total correlations (Table 10, col. 2). Since it has already been argued that recipient's weight characterises reasonably well the maternal environment she provides, the conclusion is that the association between birth weight and cannon length is not induced by the different recipient ewes providing different maternal environments, and is therefore likely to be largely genetic.

This conclusion is substantiated by a comparison of the partial regressions within subgroups with the genotypic and with the maternal regressions found from group means. The within-group partial regressions ($1 \cdot 9 \pm 0 \cdot 3$ lb. per cm. on average) are similar in magnitude to the genotypic regressions in the Blackface environment (2·0 lb. per cm.) and show no great deflection in the direction of the maternal regressions—which are about 8 lb./cm. for Lincoln lambs but which could not be estimated for Welsh lambs because their mean cannon length was not maternally affected. It may be noted that the genotypic regressions are 0·7 to 0·8 lb. per cm. greater in the Lincoln maternal environment than in the Welsh or Blackface, which are both about 2 lb. per cm.—an obvious consequence of the greater susceptibility of birth weight than of cannon length to maternal influence. Thus the ratio of birth weight to cannon length provides another example of genotype-environment interaction.

TABLE 10

Correlations of birth weight and cannon length for lambs born to Blackface recipients

	Total correlation	Partial correlation holding recipient's weight constant
Lincoln ♂	0·78	0·68
♀	0·69	0·69
Welsh ♂	0·53	0·49
♀	0·48	0·46

It was suggested earlier that selection for cannon length at birth was a more efficient means of changing mature (genetic) size than was selection for birth weight. It can now be added that the only reason that birth weight had any efficiency at all was that it was to some extent an indirect measure of cannon length, whereas no part of the cannon length-mature weight association was mediated through birth weight (partial correlation of mature donor weight with birth weight for constant cannon length was $-0 \cdot 13$ and with cannon length for constant birth weight was 0·45). Thus the full combined efficiency of birth weight and cannon length is contained in cannon length alone. Since the correlations of birth weight and cannon length are higher for Lincoln lambs than for Welsh lambs, and since the growth of Lincoln lambs was restricted by the Blackface maternal environment, it may be that birth weight is better as an indicator of cannon length in a poor environment than in a good environment. If so, selection for birth weight would change mature size more efficiently in a poor environment than in a good environment, but selection for cannon length—which is little affected by environment—would be more or less equally efficient in both environments.

DISCUSSION

The genotype of the lamb was found to be the most important factor affecting mean size at birth. Hunter (1956) gave mean values for birth weight, cannon length and gestation length for 8 lambs born as a result

of egg transfer between Welsh Mountain and Border Leicester sheep and for 7 purebred control lambs. Although his data were insufficient for firm conclusions, the observed trends are in complete accord with our results on Lincoln and Welsh. It would not be correct, however, to expect the relative importance of the maternal and genetic contributions and their interactions always to be as found in these particular cases. The partition of the total variation will depend very largely on the specific breed combinations chosen. In view of this, a partition of variation is of limited use in formulating a general understanding of maternal-foetal relationships.

In our first experiment the maternal-foetal interaction arose because large embryos (Lincoln) developing in relatively large mothers (Lincoln) were obviously bigger than in a relatively restrictive maternal environment (Welsh), while small embryos (Welsh), when given greater environmental latitude than is normal, apparently made only little use of this. In our second experiment, where Blackface gimmers provided a common maternal environment for Lincoln and for Welsh lambs, it can be deduced that the former were smaller than normal Lincoln lambs at birth and the latter were similar in size to normal Welsh lambs under the prevailing farm conditions. Thus, in their normal maternal environment, and with ewes under reasonable conditions of feeding, the mean size of single lambs at birth is likely to be near its upper genetic limit. This conclusion is supported by work done on the nutritional status of the ewe. Pálsson and Vergés (1952), for example, showed that in Suffolk cross sheep the birth weight of singles from mothers fed on a very high plane of nutrition during the second half of pregnancy was no greater than the birth weight of singles from mothers fed on a moderate plane. On both planes singles had presumably reached their upper genetic limit. When mothers were fed on the very high plane, twins also reached their limit since on average a twin weighed little less than did a single, but twins from moderate plane mothers were considerably lighter than singles.

By contrast, the limits of maternal capacity appear to be wide—large genotypes (e.g. Lincoln) were invariably bigger at birth than small genotypes (e.g. Welsh) when reared in the same maternal environment; and twin embryos, which can for these purposes be assumed to represent twice the genetic demand of a single embryo, have a bigger total birth weight than any single of the same breed. Although we have not found an upper limit of maternal capacity, the law of diminishing returns can be seen to apply in our experiments. Thus an upper limit to maternal capacity can be postulated even though other factors such as mortality will probably come into play before the theoretical limit to a ewe's total birth weight capacity is reached.

Since twins can be regarded as exerting twice the genetic demand made by a single lamb, triplets as exerting a threefold demand, and so on for larger litters, an extended range of birth weight comparisons are available from egg transfer experiments where control of number and randomisation of donor and recipient are possible. Under normal circumstances, however, such comparisons require qualification since it can be argued that ewes naturally having more than one lamb may be genetically or nutritionally different from ewes having singles. Our results lead us to expect that 2 Welsh eggs transferred into a Lincoln recipient would each develop into a lamb of nearly the same average birth weight as that of a transferred Welsh

single. Lincoln 'twins' transferred into Welsh recipients should, however, fall well below the weight of similarly transferred Lincoln singles.

Thus far, breed has been used to specify the maternal environment and the magnitude of genetic demand. Weight of ewe if taken as an index of maternal environment for single-born lambs appeared, however, to be broadly adequate in our experiments, but in specific cases there is no means of knowing just how efficient a criterion this is. For example in our own data, as shown earlier, first parity Blackface mothers, although heavier than fourth parity Welsh mothers, yielded somewhat smaller lambs. But while the limitations of weight as a predictor of maternal capacity and of genetic demand cannot be ignored, our data fit reasonably into a model where lamb's birth weight (W lb.) is envisaged as depending on mature weight of donor (D lb.) and of recipient (R lb.) and on the multiplicity of birth (m).

Thus $$W = 0.181D^{0.83}\left\{1-10^{-\frac{1.1}{m}\left(\frac{R}{D}\right)^{0.83}}\right\}.$$

The constants were estimated from the group means for female lambs born in Experiment 1 (females were 90% of male weight in Blackface, 89% in Welsh, and 86% in Lincoln mothers). They apply only to mature ewes that have more or less maintained their weight during the second half of pregnancy. No allowance is made for changes in gestation length. The model, if applied to crossbred lambs, would require the donor's mature weight to be replaced by some estimate of the crossbred lamb's own mature weight and some allowance would be necessary if there is hybrid vigour at birth not persisting to maturity. Within these limitations the model yields mean birth weights of the right order of magnitude.

Some implications of the model are of interest : at birth, in their own maternal environment, twins are expected to be 78% and triplets 62% of the mean weight of singles; the genetic limit to mean birth weight is only about 10% above the mean weight of singles in their natural mothers in a good environment; the limit of maternal capacity is reached at an average birth weight somewhat under three times that of *normal* single-born lambs; in order to halve the weight of a single-born lamb, it must be transferred into a recipient, one-quarter the weight of its natural mother. Further, the magnitude of the within-group regressions on recipient's and donor's (genetic) weight, can be deduced from the model—and for randomised egg transfer this can be done without introducing any more information than the *mean* mature weight of donor and of recipient ewes. Thus the within-group regressions of lamb's birth weight on donor's (genetic) weight are predicted as 0·015 lb./lb. for Lincoln females and 0·025 lb./lb. for Welsh females, and on recipient's weight as 0·034 lb./lb. and 0·011 lb./lb. respectively for Lincoln and for Welsh female lambs.

This investigation has shown that the prenatal growth of a lamb is neither a wholly passive process in which the growth is entirely dictated by the maternal environment nor is it a process entirely controlled by the activity of the lamb's genotype irrespective of the environmental circumstances. When dealing with *mean* size of a group of lambs a few factors appear to describe the process sufficiently well to allow reasonable prediction within the limitations specified above. About any predicted mean, however, there remains considerable individual variation in lamb's size.

SUMMARY

The influence of maternal and genetic factors on the size of lambs at birth and on their gestation length has been studied from the results of two experiments involving the transfer of fertilised eggs from one breed of sheep to another. In the first experiment, eggs were transferred reciprocally between old ewes of the large Lincoln breed and of the small Welsh Mountain breed. Results are based on 20 transfer lambs and 14 normally born singles. In the second experiment, 35 pure Lincoln and 28 pure Welsh lambs were born as a result of transferring eggs into 18-month-old nulliparous Scottish Blackface sheep.

The breed type of the lamb was found to be the most important factor influencing weight and cannon length at birth, although maternal-foetal interactions were present. As the maternal environment became poorer, genotypic differences remained distinct but decreased in magnitude. The maternal environment provided by 4th parity Lincoln ewes, if judged by lamb's size at birth, was better than that provided by 4th parity Welsh ewes, and this in turn was better than that provided by 1st parity Blackfaces. Lincoln and Welsh lambs in the same maternal environment differed in average birth weight by 5·7, 3·8 and 3·0 lb. respectively in the Lincoln, Welsh and 1st parity Blackface maternal environments. Lincoln and Welsh lambs, each in their own normal maternal environment, differed by 6·5 lb. The maternal influence on cannon length was similar but small. Gestation length of Lincoln lambs in Welsh recipients was almost 4 days shorter than that of Welsh lambs in Lincoln recipients. In the Blackface maternal environment, Lincoln and Welsh lambs differed little in gestation length but males were, on average, carried about a day longer than were females.

At the individual level, weight of (Blackface) recipient ewe had a somewhat greater effect on lamb's size than had weight of (Lincoln or Welsh) donor ewe. The magnitudes of these 'genetic' and 'maternal' effects were comparable with those found at the level of group means; even so, donor's and recipient's weight together accounted for only a small part of the individual variation in lamb's size about the group means.

It was concluded that a ewe was able to respond to progressively greater demands made by a lamb or lambs of progressively larger (combined) potential size—but in accordance with the law of diminishing returns—and that the upper limit of maternal accommodation must be considerable. By contrast, the upper limit of mean genetic size at birth appears to be not far above the mean size of single lambs born to their natural mothers in good condition. A model has been constructed from which mean birth weight of lambs can be predicted.

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Supernumerary teats in cattle

Von Gerald Wiener

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The early literature on supernumerary teats was summarised by Gifford (1934a) who showed that the frequency in females varied between 20 % and 69 % for various breeds and countries. Later estimates fall within this range (Ledenev [1952]; Pohl [1956]; Johansson [1957]; Meshchaninov [1957]; Schmahlstieg and Smidt [1958]; and Skjervold [1960]). All reports agree that caudal teats (to the rear of normal teats) are the most common (e. g. 95 %, Gifford [1934a]), while intercalary teats (between the normal front and rear teats — 5 % [ibid.]) and ramal teats (attached to the normal) are comparatively uncommon.

Generally, supernumerary teats are regarded as a nuisance because (1) they blemish the udder, (2) they can, when associated with glandular tissue be a focus for mastitis infection (e. g. Turner [1952]) and (3) they may, if attached to the principal teats, interfere with milking. For these reasons, supernumerary teats are often cut off, especially in calves. Advantages, however, including higher milk yield and better reproductive capacity, have been claimed for cows with supernumerary teats. For example Ivanova (1928) and Ledenev (1952) claimed higher milk yield for cows with extra teats but Mackenzie and Marshall (1925), Juler (1927), Gifford (1934b) and Meshchaninov (1957) found no significant yield difference between cows with four teats and those with more. Schmahlstieg and Smidt (1958) investigated 1,371 black-pied cattle in Germany (of which 30 % had supernumerary teats) and found significant differences in reproductive performance between cows with and those without supernumerary teats.

The mode of inheritance of supernumerary teats has received some attention. Juler (1927) claimed that the evidence was consistent with a simple recessive gene whilst Ivanova (1928) favoured a single dominant gene. Tuff (1950) suggested that the presence of intercalary teats was dominant. Johansson (1957) calculated a heritability of 0.23 for the total number of supernumerary teats in cows of the Swedish Red and White breed and Skjervold (1960) calculated a heritability of 0.176 for a character compounded of number and size of caudal teats on one side of the udder in Norwegian Red and White cattle.

The present study deals with the frequency and inheritance of supernumerary teats, their association with age at calving and with milk yield, and the relationship of observations in young calves with later observations on the same animals. This latter aspect has been largely neglected in previous investigations. Samples of the Ayrshire and British Friesian breeds and their crosses are described for the first time.

Material and Methods

The data are derived from two experimental herds of cattle on two of the farms of the Animal Breeding Research Organisation. One herd, at Cold Norton in Staffordshire (CN), consists of pure-bred Ayrshire (A), British Friesian (F) and Jersey (J) cattle and all possible first crosses. The sires of the females were bulls at Milk Marketing Board artifical insemination centres. Since the average number of daughters in a sire family in this herd was only about 2, there was no advantage in grouping into sire families. Observations on supernumerary teats were made when the females were about one week old, again at the age of six months and for a third time six weeks after the start of the first lactation (about 27 months old). The second herd, at Blythbank, Peeblesshire (BB), consists of pairs of female twins of one-egg (MZ) and of two-egg (DZ) origin; pairs of full sisters – the female offspring of one bull mated to a pair of one-egg twins – (FS); pairs of paternal half-sisters (HS); and pairs of unrelated females (U) born within a few days of each other and reared together – as were the members of all other pairs. Several breeds are involved, principally Ayrshire, Friesian, Shorthorn and miscellaneous crosses, and, broadly speaking, they are balanced between the various classes of pair (MZ, DZ, FS, HS) except the unrelated ones (U) which are of the Ayrshire type only. Examination for supernumerary teats took place, as in the other herd, when calves were about a week old, and a proportion of the animals were seen again on the third of the occasions described above.

Indications for supernumerary teats were hairless protuberances, however small, visible on the exterior of the udder in addition to the four principal teats. All observations were made by technical staff on the farms but the same person did not necessarily take all the observations on each animal. In herd BB, supernumerary teats were cut off (if of sufficient size) in the week-old calves but remaining scar tissue was counted as indicating presence of supernumerary teats at the next observation.

Results

Frequency and placement

Caudal teats accounted for about 94 % of all supernumeraries observed, intercalary teats for a further 5 % and ramal teats for about 1 %. Ramal teats were not noticed in young calves but were seen attached to normal teats of some females at six months old and to those of a few more of the animals examined during lactation. Table 1 shows the proportion of calves at a week old according to the number of caudal and intercalary teats observed. In both herds more than a third of the animals had at least one caudal teat. Only one member of each twin pair or full-sister pair in herd BB has been used in compiling the frequency distribution in order to avoid bias if supernumerary teats are inherited. The frequencies of supernumerary teats quoted in Table 1 include errors of observation and recording and may not be the same as the "real" number of teats present – or likely to be present at later ages. This point will be referred to again. The frequencies recorded at later ages (6 months, and 6 weeks after start of 1st lactation) differed only slightly from those shown in Table 1 for calves of one week old (see later). Since

supernumerary teats in the caudal position are the most frequent and the only ones distributed among all sub-groups in our data, further consideration will be given mainly to these caudal teats.

Table 1

Percentage frequency of female calves (about 1 week old) with supernumerary teats

Herd	Number of animals	Position of teats	Number of supernumerary teats				
			0	1	2	3	4
CN	277	Caudal	62.5	21.3	15.5	0.7	0.0
		Intercalary	96.4	3.2	0.4	0.0	0.0
BB[1]	546	Caudal	66.1	18.5	14.5	0.7	0.2
		Intercalary	97.4	2.6	0.0	0.0	0.0

[1] only one member of each twin pair and full-sister pair has been included.

Caudal teats were found as often on the right as on the left side of the udder (Table 2). If the placement of caudal teats on the right and on the left side of the udder were independent, only 48 %, instead of the observed 80 %, of calves would have had the same number of supernumerary teats (0, 1, 2 or 3) on each side of the udder. Thus when two or more caudal teats were seen, they were, with one exception, found on both sides of the udder (the single exception shown in Table 2 – two teats on the right side with none on the left – may well be due to an observational or a recording error since the same animal when seen next at 2¼ years old was recorded as having only one caudal supernumerary teat). There is therefore a strong tendency for bilateral symmetry in the occurrence of caudal supernumerary teats. Further analysis is confined to the total number of such teats.

Table 2

Placement of caudal supernumerary teats on udder (data from CN and BB[1] herds combined)

		Right side		
	number of teats	0	1	2
Left side	0	534	82	1
	1	78	121	2
	2	0	4	1

[1] only one member of each twin pair and full-sister pair has been included.

Concordance in the number of caudal supernumerary teats at different ages

Table 3 shows the number of caudal supernumerary teats recorded at three ages for the same animals. The agreement between ages 1 and 3 was slightly

higher in the CN herd (82.7 %) than in the BB herd (76.6 %). The lower concordance in the BB herd might be due to the practice in this herd of removing supernumerary teats from calves but if so, this is not reflected by extra errors of omission at the later age since there was actually a net increase in the number of supernumeraries recorded between ages 1 and 3. The data from the CN herd show that agreement between ages 2 and 3 was slightly higher than between either of these and age 1 – suggesting a greater degree of observational error at the calf stage. Agreement between all three ages, however, occurred in more than three-quarters of the animals examined.

Table 3

Concordance in the number of caudal supernumerary teats at different ages

Number of teats recorded	% of observations recorded as alike at ages[1]				
	all 3	1+2 (CN herd)[2]	2+3	1+3	1+3 (BB herd)[3]
0	54.2	56.0	57.4	56.4	54.2
1	11.9	14.8	15.5	13.3	12.1
2 or more[4]	10.5	11.6	14.5	13.0	10.4
Total agreement	76.6	82.4	87.4	82.7	76.7

[1] age 1 = 1 week old or less, 2 = 6 months old, 3 = 6 weeks after start of 1st lactation.
[2] observations on 277 females (CN).
[3] observations on 193 females and including only one member of each twin and full-sister pair (BB).
[4] 5 animals with 3 recorded supernumerary teats included as 2.

A record of a particular number of supernumerary teats may be regarded as compounded of two parts – a "real" presence (or absence) of supernumerary teats on the udder and a probability of correctly recording that fact. For example, a recorded zero (no supernumerary) can be thought of as: $P_0p_{00} + P_1p_{10} + P_2p_{20} + \ldots$ (where P_0, P_1, P_2, are the probabilities that what is really present on the udder is 0, 1, or 2 supernumerary teats while p_{00} is the probability of recording a "real" 0 as a 0, p_{10} the probability of recording a "real" 1 as a 0, etc.).

By this argument and a process of iteration, probabilities were deduced from the data in Table 3 for the actual occurrence of different numbers of caudal teats and of recording them correctly. Thus the probable proportions in the CN herd were:

0 Caudal teat	60 %
1 Caudal teat	21 %
2 Caudal teats or more	19 %

(The distribution in the BB herd was probably not very different.) The probabilities of recording correctly were approximately as follows:

	Calves (age 1)	later ages (2 or 3)
0 Caudal teat	95 %	97 %
1 Caudal teat or more	75 %	88 %

From these estimates it is seen that the probability of correctly recording an absence of caudal teats was very high at any age. The probability of cor-

rectly recording the presence of a caudal supernumerary teat though as good as 75 % in calves of about a week old, had improved substantially by the time the animals were six months old.

The repeatability (r) of the number of caudal teats between ages 1 and 3 was 0.78 for females in the CN herd, and 0.64 for females in the BB herd.

The data are not adequate to distinguish the three possible causes of discordance viz. additions or resorptions of teats and observational errors. However, the proportion of lactating heifers recorded with supernumerary teats was slightly greater (0.7 % at CN and 3.2 % at BB) than the proportion among the same animals seen as one-week-old calves. The total number of supernumerary teats recorded for the heifers exceeded the number recorded for the calves by 2.4 % at CN and 10 % at BB. This shows that additions to the number of supernumeraries present in calves and errors of omission at that stage exceed the combined effects of resorptions and errors of recording too many teats in calves. The difference between the herds suggests, however, that errors predominate.

Effect of Breed

Table 4 shows the incidence of caudal supernumerary teats for calves in each of the three pure breeds and their three crosses in the CN herd. Reciprocal crosses have been pooled.

Table 4

Incidence of caudal supernumerary teats according to breed (CN herd) in female calves (about 1 week old)

No. of teats	% females per breed type[1]					
	Ayrshire	Friesian	Jersey	AF	AJ	FJ
0	52.4	68.3	86.7	59.4	59.2	58.8
1	28.6	14.6	0	20.3	27.8	27.5
2+	19.0	17.1	13.3	20.3	13.0	13.7
Total number of animals	42	41	30	59	54	51

[1] reciprocal crosses pooled.

A X^2 test for breed heterogeneity indicated that differences between the six breed types in the proportion of animals with or without caudal teats did not quite reach statistical significance at the 5 % level of probability. However, the relatively large contribution of the Jersey group to the total X^2 value suggests that if any breed were eventually found to differ from the others it would most likely be the Jersey.

The average measure of breed variation in the frequency of animals with caudal teats was virtually unchanged at the age of 27 months, although there were some changes in the proportions with supernumerary teats among individual breed types. For example 20 % of the Jersey heifers were recorded with caudal supernumeraries.

Pure-bred and cross-bred cattle did not differ significantly in the frequency of animals with caudal supernumerary teats.

Jersey, Holstein and Guernsey cows, as well as cows in a "miscellaneous" breed group, were included in GIFFORD's (1934a) study. These breed groups differed significantly in the proportion of cows with supernumerary teats. JOHANSSON (1957) has reported significant differences in the frequency of supernumerary teats of two Swedish breeds of cattle.

Inheritance of number of caudal supernumerary teats

The BB herd of cattle consists of pairs with differing genetic relationship all maintained under a uniform system of management (see DONALD [1953]). Table 5 shows the distribution of caudal supernumerary teats in paired female calves (about one week old).

A total of 227 pairs of MZ twins collected as calves by the Animal Breeding Research Organisation over a period of about ten years were available for this study. Concordance in the number of supernumerary teats played a part, however, in the earlier years of collection in diagnosing twins as one-egg or two-egg. As experience in twin diagnosis grew, supernumerary teats came to be ignored. Hence to avoid bias in the interpretation of MZ data, only the last 100 MZ twins collected have been used in analysis (the first 100 such twins showed concordance in 81 % of pairs, whereas the last 100 showed 73 % concordance).

Table 5

Percentage distribution of caudal supernumerary teats in pairs of female calves (about 1 week old) of different relationship (BB herd)

pair pattern in number of teats	type of pair MZ[1]	DZ	FS	HS	U
00	56.0	46.1	16.7	50.0	36.9
11	4.0	10.3	8.3	1.9	2.6
22	13.0	2.4	8.3	3.8	7.9
01	15.0	22.2	25.0	23.1	21.1
12	7.0	7.9	12.5	7.7	2.6
02	5.0	8.7	25.0	11.6	28.9
Others[2]	0	2.4	2.1	1.9	0
concordant[3]	73.0	58.8	33.3	55.7	47.4
discordant[4]	27.0	41.2	66.7	44.3	52.6
Total number of pairs	100	126	24	52	38

[1] only the last 100 (out of total of 227) pairs of MZ twins considered – see text.
[2] Other pair patterns found were 13, 23, 03.
[3] concordant pairs = 00, 11, 22.
[4] discordant pairs = 01, 12, 02, others.

Concordance in the number of caudal supernumerary teats increased with the increasing closeness of genetic relationship of pairs (except FS) as Table 5 shows. This suggests that the trait is inherited. Estimates of heritability (h^2) were made by the techniques advocated for continuous variables although it is not known to what extent this is legitimate for a character such as number of supernumerary teats. Table 6 shows the values of mean squares for the five types of pair.

Table 6

Analysis of variance of number of caudal supernumerary teats in paired female calves (about 1 week old) of different relationship (BB herd)

type of pair	Number of pairs	Within-pair M. S.	Between-pair M. S.	Total M. S.
MZ	100	0.21	1.06	0.63
DZ	126	0.41	0.66	0.53
FS	24	0.71	0.90	0.80
HS	52	0.47	0.69	0.58
U	38	0.70	0.74	0.72

Five components of variation were isolated, namely effects of environment (e^2), additive genetic effects (g^2), effects of dominance deviations from additive genetic effects (d^2), the effects of being born a twin as compared with a single (m^2), and the combined effects of breed variation and contemporary birth ($b^2 + c^2$) which are confounded in these data (cf. KING and DONALD [1955]). It might be suggested that e^2 as estimated from the within-pair variation of the MZ twins (0.21 ± 0.03) would still be too small despite the precaution of using the data of the last 100 pairs only. However, there is evidence that this bias does not occur in the present data. A weighted least squares method was used to estimate the five components from the ten items of information given by the within- and between-pair mean squares (M.S.) shown in Table 6. Although these items are independent, they are not of equal weight – partly because of the different numbers involved. For this reason each item was roughly weighted by its sampling variance. The estimates for each of the five components are as follows:

$$e^2 \quad 0.21 \pm 0.03$$
$$g^2 \quad 0.45 \pm 0.64$$
$$d^2 \quad 0.01 \pm 0.44$$
$$m^2 \quad -0.03 \pm 0.11$$
$$(b^2 + c^2) \quad -0.05 \pm 0.16$$

total variance (sum of all 5) 0.59 ± 0.03.

These five components together removed all but an insignificant proportion of the variation in the mean squares (the χ^2 test for goodness of fit was only approximate). Individually, d^2 and g^2 both have large standard errors, but the estimate of total genetic variation and its standard error was 0.46 ± 0.22. Therefore a significant amount of genetic variation is present but since individually g^2 was considerable and d^2 negligible and both cannot be estimated with accuracy, it seemed legitimate to exclude d^2 from further consideration. Also m^2 and $(b^2 + c^2)$ might reasonably be ignored because they were found to be very small, statistically insignificant and negative.

Thus only e^2 and g^2 were reconsidered as being important. The fit to the set of mean squares was every bit as good (by the same approximate test) when using these two items alone as when using all five, the residual sum of squares being insignificant.

The new estimates are:

$$e^2 \quad 0.22 \pm 0.03$$
$$g^2 \quad 0.37 \pm 0.04$$

The total variance is estimated, as before, as 0.59 ± 0.03 and can be compared with the direct estimate (pooling all classes) of 0.61 ± 0.03. The estimate of e^2 is also practically unchanged.

Thus the evidence points to the genetic variance being additive and a heritability (h^2) was calculated for the number of caudal supernumerary teats in female calves of one week old as:

$$h^2 = 0.63 \pm 0.05.$$

The standard error of this estimate is an approximation deduced from weighted residual variation but its smallness is not unreasonable in view of the precision with which e^2 is estimated directly (from MZ) and the precision with which the direct pooled estimate of total variance is endowed.

Although the component for breed variation (b^2) — confounded with the contemporaneity factor (c^2) — was small and insignificant, the analysis as described above was repeated for the pairs of calves belonging to the Ayrshire breed alone (38 pairs of MZ, 38 DZ, 21 HS, and 38 U). The estimates of total variation and of the individual components were in close agreement with those derived from the larger number of pairs comprising several breeds (including the Ayrshire). The estimate of h^2, derived as above but for the Ayrshire group alone, was 0.61 ± 0.06.

For older animals the slightly greater accuracy with which the number of their supernumerary teats was observed would lead to higher heritability estimates than those for the week-old calves.

Relationship to heifer performance

The total number of supernumerary teats (caudal and intercalary combined, but excluding ramal teats) were studied in relation to age at first calving and to first lactation milk yield (limited to 305 days) for the animals in the CN herd. Within breed types there were differences in performance between heifers having no supernumeraries and those having 1 or 2 (for present purposes those with more than 2 supernumerary teats were included with the class having 2). Some of these differences seemed quite large (e. g. in the Jersey group the heifers with one supernumerary teat calved about 12 weeks later and yielded 246 gal. more milk than those without supernumerary teats,

Table 7

Relationship of supernumerary teats[1] to age at first calving and first-lactation milk yield (CN herd)

Supernumerary teat classes[3]	differences[2] (and their S. E.'s) for age at 1st calving (days)	Milk yield (lb. × 10)
0—1	5±11	7±39
0—2 or more	2±11	14±39

[1] Caudal and intercalary teats combined.
[2] Differences for individual breed types pooled after allowing for number of animals and variance of differences.
[3] Yields (and ages) of animals with supernumerary teats (1 or 2) subtracted from those of animals without supernumeraries. Animals with more than 2 supernumeraries have been included in the (2) class.

whilst in the Ayrshire group the equivalent differences were 3 weeks and 132 gal. – but in the opposite direction) but only the two or three extreme differences approached an acceptable level of statistical significance ($P = 0.05$). Breed types were pooled by weighting each difference by the reciprocal of the variance of the difference. The results in Table 7 show that on average the heifers with supernumerary teats calved for the first time a few days earlier than those without such teats and yielded a few gallons less milk, but these small differences have large standard errors. Consequently no significant association between supernumerary teat numbers and these two aspects of performance can be demonstrated.

Discussion

Some two-fifths of the cattle examined in this study were found to have at least one supernumerary teat, generally of the caudal type. This incidence falls almost mid-way in the range recorded over the past sixty years in other breeds and countries. There is a remarkable degree of bilateral symmetry of supernumerary teats. This is displayed by the absence of asymmetric distributions when two teats were present and, on the basis of random placement, by a deficiency of animals with one supernumerary teat and an excess with no supernumeraries. This phenomenon can also be found in the data tabulated by GIFFORD (1934a) and by SKJERVOLD (1960). Among the cows recorded by SKJERVOLD, bilateral symmetry can be seen to extend – though less strongly – to the size of the supernumerary teats.

It has been shown that there is fair agreement between the number of caudal teats seen in week-old calves and the number recorded for the same animals as adults. It follows from this and from the fact that the number of caudal teats appears to be quite strongly inherited, that the incidence in the population could be altered fairly rapidly by selection. However, there is no evidence in the literature, apart from the report by SCHMAHLSTIEG and SMIDT (1958), of an association between the number of teats and fertility in cattle and in the present study there was no significant association with age at first calving. Since cows usually have only one calf at a time, the number of teats does not limit rearing ability. It is also unlikely that the normal number of teats sets any limits on total milk production under present-day systems of management. Our data show no significant association between the number of supernumerary teats and milk yield. The cattle breeder thus seems to have no cause to select for extra teats. In any event it would be more difficiult to select for extra teats associated with glandular tissue than to select for number alone. SKJERVOLD (1960) calculated a heritability of 18 % for a character compounded of number and size of supernumerary teats on each side of the udder in the Norwegian Red and White breed. Only a small proportion of these were ducts for milk glands. JOHANSSON (1957) gave a heritability estimate of 23 % for the simpler character of the total number of supernumerary teats on the udder in the Swedish Red and White breed. The estimate from our data of mixed breed origin (Ayrshire, Friesian, Shorthorn, and miscellaneous crosses) was much higher ($h^2 = 63$ %). There is evidence which suggests that the inclusion of several breeds did not, however, inflate the estimate of genetic variation. For the Ayrshire breed alone our estimate of heritability was 61 %. Reduction of the number of super-

numerary teats may be a legitimate aim of breeders and if cutting off such teats is not considered an adequate method, selection ought to be effective.

Zusammenfassung

Die Euter von 823 weiblichen Kälbern im Alter von 1 Woche wurden auf Mehrzitzigkeit untersucht und bei 38 % eine und mehr überzählige Zitzen festgestellt. Der Anteil von caudal überzähligen Zitzen betrug 94 %. Das Auftreten der Mehrzitzigkeit war auf der rechten und linken Euterhälfte gleich. Caudal befindliche überzählige Zitzen zeigten eine strenge bilaterale Symmetrie in ihrer Anordnung. Eine zweite Untersuchung der Tiere wurde im Alter von 6 Monaten und eine dritte 6 Wochen nach der ersten Kalbung durchgeführt. Die Wahrscheinlichkeit für die richtige Erfassung der Anzahl der Zitzen variiert mit dem Alter der Tiere und mit dem Auftreten von Mehrzitzigkeit. Am geringsten ist diese Wahrscheinlichkeit bei Kälbern mit überzähligen Zitzen (0,75) und am höchsten bei laktierenden Tieren ohne überzählige Zitzen (0,97). Bei den Unterschieden zwischen den Rassen konnte für die caudal überzähligen Zitzen die 5 %-Grenze der Irrtumswahrscheinlichkeit nicht ganz erreicht werden. Für diese Mehrzitzigkeit konnte bei Kälbern im Alter von 1 Woche eine Heritabilität von $0{,}63 \pm 0{,}05$ errechnet werden. Dominanz spielt keine wichtige Rolle. Die Zahl der überzähligen Zitzen war mit dem Erstkalbealter oder mit der Milchleistung nicht signifikant verbunden.

Summary

The udders of 823 female calves at about 1 week old were examined for presence of supernumerary teats and 38 % were found to have at least one. About 94 % of the supernumerary teats were of the "caudal" type. Such teats were found as often on the left as on the right side of the udders. Caudal supernumerary teats showed strong bilateral symmetry in their placement on the udder. A proportion of the animals were seen for a second time at the age of six months, and for a third time, six weeks after the start of their first lactation. The probability of correctly recording the number of caudal teats varied with the age of the animals and with the presence or absence of caudal teats — being lowest for the calves with supernumeraries (0.75) and highest for the lactating heifers without any extra teats (0.97). Differences between breeds in the proportion of animals with caudal supernumerary teats did not quite reach statistical significance at the 5 % level of probability. A heritability (h^2) of 0.63 ± 0.05 was calculated for the number of caudal teats observed in calves about one week old. Dominance did not play an important part. The number of supernumerary teats was not significantly associated with age at first calving or with milk yield.

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MATERNAL AND GENETIC INFLUENCES ON FOLLICLE AND FLEECE DEVELOPMENT IN LINCOLN AND WELSH MOUNTAIN SHEEP—A STUDY INVOLVING EGG TRANSFER

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THIS paper describes the effects of unusual maternal environments on the follicle and fleece development of lambs. The experiment involved the transfer of fertilised sheep eggs from Lincoln to Welsh Mountain ewes and vice versa. As adults, these breeds differed greatly in size and the weight of the Lincoln was about twice that of the Welsh Mountain when both were kept under the same conditions. Egg transfer thus offered a technique for obtaining wide maternal-foetal body size ratios with a controlled litter size. The body size at birth of the lambs in this experiment was reported by Dickinson, Hancock, Hovell, Taylor and Wiener (1962).

Maternal influences on follicle development and fleece growth in sheep have been studied principally in the Merino by using different levels of maternal nutrition. In that work, maternal factors were found to have affected secondary follicle development and fleece growth presumably because development and maturation of secondary follicles was particularly active in the last six weeks before and the first six weeks after birth (Short, 1955*a*, 1955*b*; Schinckel and Short, 1961). Doney and Smith (1964) found temporary differences in secondary fibre number when comparing twin-born with single-born lambs in the Scottish Blackface breed of sheep.

MATERIAL AND METHODS

Animals. The Lincoln and Welsh Mountain sheep used had been born and bred in their native regions in England and Wales, but from the age of six months had been reared on the Animal Breeding Research Organisation's farm of Blythbank in Peeblesshire. At the age of 4½ years when the ewes had had three normal lamb crops they were mated to their own breed of ram. Fertilised eggs were recovered and transferred reciprocally between the two breeds—one egg per recipient. Females surplus to requirements as donors were mated to their own breed of ram to produce lambs by normal means (control group). Twins were born to 6 of the 13 ewes in the control group. Only one Lincoln ram was used and all but two of the Welsh lambs were the offspring of the same Welsh sire.

The egg transfer technique used in this experiment has been described by Hancock and Hovell (1961) who performed the operations.

The two breeds of ewe and of lamb were run as a single flock on grass both before and after lambing which occurred in April and May. Further details of management were given by Dickinson *et al.* (1962).

Sampling. Skin samples were taken within 8 days of birth (with a smaller range within class of lamb) and again at 84 days of age ($\pm 3\frac{1}{2}$ days) from the right mid-side with a skin biopsy punch 1 cm. in diameter. Fleece samples

were taken at 84 days old from the right mid-side by close-clipping an area of 10 cm^2 delineated with hair-pin calipers.

The skin sections were used to estimate follicle density, i.e. the number of primary and secondary follicles per unit area (expressed as the mean of four counts), medullation of primary and secondary fibres (the number medullated among 25 fibres of each type) and fibre diameter. For the counts all follicles including immature secondaries were scored. The 84-day fleece samples were weighed and 50 fibres picked at random were measured for length.

The methods of sampling and processing were substantially those described by Carter and Clarke (1957).

Randomisation. There were small random differences between the different groups (as shown in Table 1) in the average age at the first skin sampling; these differences might introduce a bias of unknown magnitude into some of the comparisons.

Non-transferred lambs (N) were born on average 19 days later than those in the transfer groups (T); this also could introduce a bias into some of the comparisons.

For each breed of ewe there were no significant differences in body size as between donor and recipient ewes or between those with normal lambs and those with lambs from egg transfer.

RESULTS

Table 1 shows the average values for the various skin and fleece characteristics at birth and 84 days. Subsequent tables show differences (with standard errors) between these average values. These differences were attributable to maternal environment as defined by the breed of dam, to the genotype (breed) of lamb, and to interactions between the lamb's genotype and the maternal environment (Tables 2 and 3). Further differences arose from the comparison (within breed of lamb and dam) of twin and single lambs (Table 4).

Data from male and female lambs have been pooled because there were few consistent or significant differences due to sex in the skin and fleece characteristics either at birth or at 84 days old—this in spite of the fact that the male lambs were heavier at birth and had longer cannon bones than the females (Dickinson *et al.*, 1962). The exceptions in the present study were medullation of primary fibres ($\bar{m}_p$), primary fibre diameter ($\bar{d}_p$) and, in consequence, the ratio of primary to secondary fibre diameter ($\bar{d}_p/\bar{d}_s$). The females in each subgroup had on average the greater number of medullated fibres and larger primary fibre diameters and diameter ratios. The average sex difference in these characteristics was statistically significant ($P<0{\cdot}05$) only at 84 days old.

The relationship between age at first sampling and the individual values for each of the skin characteristics was looked at by means of scatter diagrams separately for each class of lamb. There appeared to be no significant relationship. Thus, the fact that the animals were not all sampled on the same day could be ignored as far as effects of age within classes are concerned. It also seemed likely therefore that the slight average differences in age at first sampling between the classes of lamb would not affect the comparisons.

The average values (Table 1), the differences between single lambs of

TABLE 1

Average estimates of skin and fleece characteristics at birth and 84 days old in lambs born to their own breed of mother (N) or as a result of egg transfer (T) (sexes combined)

Category	N	T	N	T	N	N	N	T	N	T	N	N
Breed of lamb	Welsh	Welsh	Lincoln	Lincoln	Welsh	Lincoln	Welsh	Welsh	Lincoln	Lincoln	Welsh	Lincoln
Breed of dam	Welsh	Lincoln	Lincoln	Welsh	Welsh	Lincoln	Welsh	Lincoln	Lincoln	Welsh	Welsh	Lincoln
Birth type	←——— Single ———→				←— Twin —→		←——— Single ———→				←——Twin——→	
Number of lambs	5	7	2	11	8	4	5	7	2	11	8	4
Mean age of sampling (days)	3·6	4·9	3·0	6·5	5·3	2·5	84	84	84	84	84	84
Follicle number (n) † per sq. mm.												
$\bar{n}_{p+s}$	64·8	53·3	54·6	44·9	66·2	58·2	26·7	24·1	20·2	16·9	26·5	22·1
$\bar{n}_p$	14·9	11·9	10·1	9·9	15·8	11·9	4·6	4·2	3·3	3·2	5·4	4·3
$\bar{n}_s/\bar{n}_p$	3·42	3·49	4·30	3·66	3·20	3·98	4·78	4·74	5·00	4·35	3·93	4·05
Number of medullated fibres (m) † per 25 fibres counted												
$\bar{m}_p$	22·6	14·9	0·5	10·6	20·5	4·3	16·8	11·4	4·0	8·1	16·5	7·5
$\bar{m}_s$	0·6	0	0	5·6	0·1	2·3	0·6	0·6	4·5	0·6	0·6	1·8
Fibre diameters (d) † in μ												
$\bar{d}_p$	54·7	48·9	27·8	34·1	56·1	28·0	58·1	44·9	35·3	41·3	48·8	38·0
$\bar{d}_s$	22·3	24·7	30·6	31·1	23·6	25·8	25·6	27·1	30·3	29·4	23·5	27·6
$\bar{d}_{p+s}$	30·4	30·4	30·0	32·2	31·4	26·4	31·3	30·2	31·1	31·9	28·7	29·7
$\bar{d}_p/\bar{d}_s$	2·45	2·05	0·91	1·11	2·37	1·10	2·27	1·65	1·16	1·41	2·07	1·39
Fleece-sample characteristics												
Wool weight (g.) from an area of 10 cm²							1·26	1·30	2·60	2·44	1·05	1·92
Fibre length (cm.)—mean of 50 fibres							3·16	4·09	6·25	7·10	3·15	6·23
Log variance of fibre length (cm²)							0·3652	0·5119	1·0045	1·0550	0·3594	0·9720

† The subscripts used are $p =$ primary and $s =$ secondary (follicles or fibres).

the egg transfer and control groups at birth (Table 2) and at 84 days old (Table 3) and the differences between control singles and twins (Table 4) will now be discussed for each group of characters.

Follicle density. As expected, follicle densities were greater at birth than at 84 days old, but the ratio of the number of secondary to primary follicles ($\bar{n}_s/\bar{n}_p$) was greater at the later age indicating that secondary follicle development was active after birth—or possibly that not all secondary follicles were visible a few days after birth at the skin level examined.

At birth, Lincoln lambs had a larger total number of follicles ($\bar{n}_{p+s}$) per sq. mm. when born from the Lincoln than from the Welsh maternal environment, and a larger number of secondary follicles relative to primaries. By 84 days old the effects on density were reduced in magnitude while the effects on the $\bar{n}_s/\bar{n}_p$ ratio were similar to those at birth.

Lincoln lambs did not differ from Welsh lambs in terms of follicle density when both were born in the Lincoln maternal environment but differed in the Welsh environment such that Lincoln lambs had the lower density, particularly at birth. The $\bar{n}_s/\bar{n}_p$ ratio showed a tendency to be higher for Lincoln lambs at birth especially in the Lincoln maternal environment. By 84 days old the $\bar{n}_s/\bar{n}_p$ ratio for Lincoln lambs in the Welsh environment had not reached the level of the ratio for those in the Lincoln environment and the relative change from birth to 84 days was smaller than for Welsh lambs.

There are thus several pieces of evidence suggesting a permanent reduction of follicle development in the transferred Lincoln lambs. The physical effects of lamb size and surface area on follicle density are likely to be in the opposite direction to the effects attributed to maternal environment in the Lincoln transfer group. Therefore the average differences in the tables and their standard errors are of only limited usefulness and probably underestimate the extent or significance of the biological effects which have taken place. These points will be elaborated later.

Lincoln lambs appear to have reacted differently from Welsh lambs to the two maternal environments; thus the average effects produced were relatively small while interactions were more important. The average effects of lamb's genotype seemed to have been more important than the average effects of the maternal environment.

The comparison between singles and twins showed a tendency for singles to have had lower follicle densities but higher ratios of $\bar{n}_s/\bar{n}_p$. For single lambs at birth, differences due to the effects of the maternal environment (transferred *v.* normal) were, by and large, greater than the differences between singles and twins when the Lincoln and Welsh breeds were compared individually. At the age of 84 days maternal differences due to egg transfer were greater than those between singles and twins for follicle density ($\bar{n}_{p+s}$) but not for the ratio $\bar{n}_s/\bar{n}_p$.

Medullation. Average values for both breeds of lamb and dam showed that a high proportion of primary fibres were medullated, but only a low proportion of secondaries. For primary fibres alone Welsh lambs had a far higher proportion with medulla than did Lincoln lambs at both birth and 84 days old and in both maternal environments. In addition, both breeds of lamb had a significantly greater primary fibre medullation in the Welsh maternal environment. There seems no obvious explanation for this. The estimate of the effect of genotype of lamb in the 'average' maternal

TABLE 2

Differences (and standard errors) in skin and fleece characteristics within a few days of birth between transferred and normal Lincoln and Welsh single-born lambs (sexes combined) †

(*a*) Effect of maternal environment (Lincoln—Welsh)

Genotype of lamb	Effect of maternal environment on								
	$\bar{n}_{p+s}$	$\bar{n}_p$	$\bar{n}_s/\bar{n}_p$	$\bar{m}_p$	$\bar{m}_s$	$\bar{d}_p$	$\bar{d}_s$	$\bar{d}_{p+s}$	$\bar{d}_p/\bar{d}_s$
Lincoln	9·7±7·3	0·2±1·6	0·64±0·78	−10·1±4·1	−5·6±3·7	−6·3±3·3	−0·5±2·7	−2·2±2·1	−0·20±0·14
Welsh	−11·5±5·5	−3·0±1·0	0·07±0·46	−7·7±2·4	−0·6±0·5	−5·8±4·3	2·4±1·1	−0·0±2·0	−0·40±0·11
Average	−0·9±7·0	−1·4±0·9	0·35±0·43	−8·9±1·5	−3·1±0·8	−6·0±3·3	0·9±2·4	−1·1±2·6	−0·30±0·07

(*b*) Effect of lamb's genotype (Lincoln—Welsh)

Maternal environment	Effect of lamb's genotype on								
	$\bar{n}_{p+s}$	$\bar{n}_p$	$\bar{n}_p/\bar{n}_s$	$\bar{m}_p$	$\bar{m}_s$	$\bar{d}_p$	$\bar{d}_s$	$\bar{d}_{p+s}$	$\bar{d}_p/\bar{d}_s$
Lincoln	1·3±8·3	−1·8±0·8	0·81±0·63	−14·4±4·1	0±0	−21·1±6·0	5·9±2·5	−0·4±3·2	−1·14±0·14
Welsh	−19·9±5·2	−5·0±0·8	0·24±0·55	−12·0±2·6	5·0±2·4	−20·6±3·0	8·8±1·5	1·8±1·5	−1·34±0·11
Average	−9·3±7·0	−3·4±0·9	0·53±0·43	−13·2±1·5	2·5±0·8	−20·8±3·3	7·3±2·4	0·7±2·6	−1·24±0·07

(*c*) Interactions between lamb's genotype and maternal environment

	Effect of interaction on								
	$\bar{n}_{p+s}$	$\bar{n}_p$	$\bar{n}_p/\bar{n}_s$	$\bar{m}_p$	$\bar{m}_s$	$\bar{d}_p$	$\bar{d}_s$	$\bar{d}_{p+s}$	$\bar{d}_p/\bar{d}_s$
Average	10·6±7·0	1·6±0·9	0·29±0·43	−1·2±1·5	−2·5±0·8	−0·3±3·3	−1·5±2·4	−1·1±2·6	0·10±0·07

† For details of number of animals and explanation of symbols and units of measurement see Table 1.

TABLE 3

Differences (and standard errors) in skin and fleece characteristics at 84 days old between transferred and normal Lincoln and Welsh single-born lambs (sexes combined) †

(*a*) Effect of maternal environment (Lincoln − Welsh)

Genotype of lamb	Effect of maternal environment on $\bar{n}_{p+s}$	$\bar{n}_p$	$\bar{n}_s/\bar{n}_p$	$\bar{m}_p$	$\bar{m}_s$	d_p	d_s	d_{p+s}	d_p/d_s	Wool weight	Fibre length	*Log* variance fibre length
Lincoln	3·3±3·1	0·1±0·5	0·65±0·44	−4·1±4·6	3·9±0·8	−6·0±4·8	0·9±2·0	−0·8±2·5	−0·25±0·15	0·16±0·27	−0·85±0·54	−0·0505±0·102
Welsh	−2·5±2·3	−0·4±0·3	−0·04±0·40	−5·4±3·0	−0·0±0·8	−13·2±7·2	1·5±1·0	−1·1±1·7	−0·62±0·24	0·04±0·13	0·93±0·38	0·1464±0·085
Average	0·4±2·8	−0·2±0·4	0·30±0·30	−4·7±2·2	1·9±0·9	−9·7±4·9	1·2±1·6	−1·0±1·7	−0·44±0·15	0·10±0·27	0·07±0·31	0·0478±0·056

(*b*) Effect of lamb's genotype (Lincoln − Welsh)

Maternal environment	Effect of lamb's genotype on $\bar{n}_{p+s}$	$\bar{n}_p$	$\bar{n}_s/\bar{n}_p$	$\bar{m}_p$	$\bar{m}_s$	d_p	d_s	d_{p+s}	d_p/d_s	Wool weight	Fibre length	*Log* variance fibre length
Lincoln	−3·9±3·7	−0·9±0·6	0·26±0·59	−7·4±3·9	3·9±1·3	−9·6±9·1	3·2±1·9	0·9±3·0	−0·49±0·27	1·30±0·30	2·16±0·42	0·4926±0·113
Welsh	−9·8±2·1	−1·4±0·3	−0·43±0·33	−8·7±3·3	0·0±0·6	−16·8±5·3	3·8±1·2	0·6±1·5	−0·86±0·18	1·18±0·13	3·94±0·38	0·6895±0·074
Average	−6·9±2·8	−1·2±0·4	−0·08±0·30	−8·0±2·2	2·0±0·9	−13·2±4·9	3·5±1·6	0·8±1·7	−0·67±0·15	1·24±0·27	3·05±0·31	0·5913±0·056

(*c*) Interactions between lamb's genotype and maternal environment

	Effect of interaction on $\bar{n}_{p+s}$	$\bar{n}_p$	$\bar{n}_s/\bar{n}_p$	$\bar{m}_p$	$\bar{m}_s$	d_p	d_s	d_{p+s}	d_p/d_s	Wool weight	Fibre length	*Log* variance fibre length
Average	2·9±2·8	0·3±0·4	0·35±0·30	0·7±2·2	2·0±0·9	3·6±4·9	−0·3±1·6	0·2±1·7	0·19±0·15	0·06±0·27	−0·89±0·31	0·0983±0·056

† For details of number of animals and explanation of symbols and units of measurement see Table 1.

TABLE 4

Differences (and standard errors) between single and twin lambs (sexes combined) in the normally-born groups for skin and fleece characteristics

(*a*) Samples taken within a few days of birth

Breed of lamb and dam	Difference between singles and twins ($s-t$) in								
	$\bar{n}_{p+s}$	$\bar{n}_p$	$\bar{n}_s/\bar{n}_p$	$\bar{m}_p$	$\bar{m}_s$	d_p	d_s	d_{p+s}	d_p/d_s
Lincoln	−3·6±10·6	−1·8±2·2	0·32±0·65	−3·8±4·0	−2·3±1·9	−0·2±3·9	4·8±4·4	3·6±4·1	−0·19±0·12
Welsh	−1·4±6·4	−0·9±1·5	0·22±0·37	2·1±2·9	0·5±0·5	−1·5±6·2	−1·3±1·9	−1·0±3·0	0·08±0·18
Average	−2·5±7·4	−1·4±1·2	0·27±0·42	−0·8±1·8	−0·9±0·9	−0·9±3·7	1·7±2·7	1·3±2·8	−0·06±0·09

(*b*) Samples taken at 84 days old

Breed of lamb and dam	Difference between singles and twins ($s-t$) in										
	$\bar{n}_{p+s}$	$\bar{n}_p$	$\bar{n}_s/\bar{n}_p$	$\bar{m}_p$	$\bar{m}_s$	d_p	d_s	d_{p+s}	d_p/d_s	Wool weight	Fibre length	*Log* variance fibre length
Lincoln	−1·9±1·0	−1·0±0·5	0·95±0·53	−3·5±5·4	2·7±1·8	−2·7±3·4	2·7±2·5	1·4±2·4	−0·23±0·09	0·67±1·09	0·02±0·41	0·033±0·045
Welsh	0·2±2·0	−0·8±0·4	0·85±0·37	0·3±2·8	0·0±0·7	9·3±6·2	2·1±0·8	2·6±1·8	0·20±0·21	0·21±0·11	0·01±0·29	0·006±0·078
Average	−0·9±2·8	−0·9±0·4	0·90±0·32	−1·6±2·5	1·4±1·0	3·3±4·5	2·4±1·6	2·0±1·9	−0·02±0·13	0·44±0·27	0·02±0·30	0·019±0·047

environment was greater than the effect of maternal environment on the 'average' genotype, but both effects were large and significant (at birth $P<0{\cdot}001$, at 84 days $P<0{\cdot}05$). The interactions by contrast were small and non-significant, as were the differences between singles and twins. Medullation of secondary fibres did not differ consistently between the various groups possibly on account of the small amount of medullation present.

Fibre diameters. Fibre diameters for the various groups of animals did not show consistent changes between birth and 84 days old, although in pooled data there was a tendency for diameter to increase with age.

The results for primary fibre diameters ($\bar{d}_p$) paralleled closely those for medullation. Welsh lambs in both maternal environments had greater primary diameters than Lincoln lambs, and the Welsh maternal environment was also associated with larger diameters than the Lincoln environment for both breeds of lamb. The effect of genotype of lamb was stronger than that of maternal environment. Both effects were quite large in relation to the mean value for the character and were significant. Differences between singles and twins were by comparison small and non-significant, as were the interactions.

Secondary fibre diameter ($\bar{d}_s$) was greater in Lincoln lambs than in Welsh lambs and there was a tendency (not statistically significant) for the Lincoln maternal environment to promote the larger diameters. As with primary diameters the genotype of the lamb was more important than the maternal environment. Differences between singles and twins, though small, were bigger than those due to differences between Lincoln and Welsh maternal environments.

The average diameter of the fibre population ($\bar{d}_{p+s}$) is heavily weighted by the preponderance of secondary fibres, and differences due to genotype of lamb, maternal environment, interaction, or singles and twins were small.

The ratio of primary to secondary fibre diameter ($\bar{d}_p/\bar{d}_s$) reflected the behaviour of its constituents. Thus at birth, genotype of lamb had the greatest effect ($P<0{\cdot}001$) whilst maternal environment had a smaller but still highly significant effect. At 84 days the effects were little changed (although smaller for genotype of lamb) but variability being greater the differences were not so highly significant. In every case the $\bar{d}_p/\bar{d}_s$ ratios involving Welsh lambs and Welsh maternal environments were greater than those involving Lincoln. Interaction terms were small and differences between singles and twins were negligible.

Fleece samples at 84 days old. For the single lambs the mean weight of wool samples from the Lincoln breed was about twice that obtained from the Welsh breed. The maternal environment had hardly any effect on weight of wool, although there may have been a tendency (not statistically significant) for the Lincoln lambs to have had very slightly more wool when born to Lincoln mothers than when born to Welsh mothers. Differences between singles and twins were, in absolute terms, quite large and, on average, about a third of the size of the breed difference, but they failed to be statistically significant.

Fibre length, measured as the mean of fifty fibres, was nearly twice as great for Lincoln as for Welsh lambs whilst singles and twins showed virtually no difference. The result of egg transfer was to increase fibre length for both breeds of lamb. Thus, the Lincoln lambs transferred to the Welsh maternal environment had longer fibres than those born in their own breed of

mother. Welsh lambs had shorter fibres when born to their own breed of dam than when born in the environment of Lincoln dams. In consequence there was a significant genotype-environment interaction. The maternal effects on fibre length had the opposite sign to the maternal effects on follicle density and the $\bar{n}_s/\bar{n}_p$ ratio. The implications of this will be discussed later.

The mean variances of fibre length were converted to logarithms since the standard deviation of mean variance was very different for the two breeds of lamb. (The standard deviation of mean *log* variance of fibre length was almost the same for each category of lamb.) The values for mean *log* variance of fibre length were about twice as high for Lincoln as for Welsh lambs, this effect being highly significant ($P<0{\cdot}001$). Maternal environment had very little influence but there was a tendency ($P = 0{\cdot}1$) for transferred Welsh lambs to have a greater fibre length variance than non-transferred ones. The interaction term although small in relation to the genetic differences was of sufficient magnitude to suggest a differential effect on the two breeds of lamb by the two maternal environments. Differences between singles and twins were very small.

DISCUSSION

The experimental situation described in the present paper offers a comparison of breed differences in a common maternal environment. This differs greatly from the usual pure-breed comparisons where genetic and maternal effects are confounded. Such a comparison in our data would be that between the two non-transferred groups—the Lincoln lambs with Lincoln mothers compared with the Welsh lambs with Welsh mothers. Such differences, although of interest, are not our chief concern here.

In the present experiment, large and persistent maternal effects coexisted with large genotypic effects such that both independent and interacting components for each effect could be distinguished.

The effects of maternal environment, both pre-natal and post-natal, can be considered in two parts—the one affecting equally all genotypes in a general way, the other specific to each genotype. In this experiment the general part is described by the maternal effect on the average of the Lincoln and Welsh lambs' genotypes, whereas the specific part is described by the interaction between lamb genotype (lamb's breed) and maternal environment (mother's breed). Within each class of maternal/foetal type, individual variation contributes to the error of estimating the average effects. In an effort to summarise the information derived from this study, components of variance were calculated from the average values of the four classes of single-born lambs and an error term was derived from the pooled within-class variance. This procedure is open to statistical argument but can be regarded as yielding an approximate estimate of the relative contributions of each source of variation as shown in Figure 1. Some generalisations emerge. For follicle densities and medullation the total effect of maternal environment seemed to be more important soon after birth than at 84 days old, whereas for the $\bar{n}_s/\bar{n}_p$ ratio and fibre diameters the reverse seemed true. Further, maternal effects appeared to be mainly specific for follicle density, the ratio $\bar{n}_s/\bar{n}_p$, and fibre length and its variance, but more equally distributed between general and specific effects for the other characters. The breed type of the lamb seemed to be the single most important influence,

in this partitioning of variation, for most of the characteristics observed at both ages. The exceptions among the total of 21 parameters were: the $\bar{n}_s/\bar{n}_p$ ratio, the average fibre diameter ($\bar{d}_{p+s}$) and, at birth only, medullation of secondary fibres and the average fibre density ($\bar{n}_{p+s}$).

A weakness of the present study derives from the small number of lambs involved, particularly in the non-transfer (control) groups. Data (Carter and Wiener, unpublished) were therefore analysed from skin and

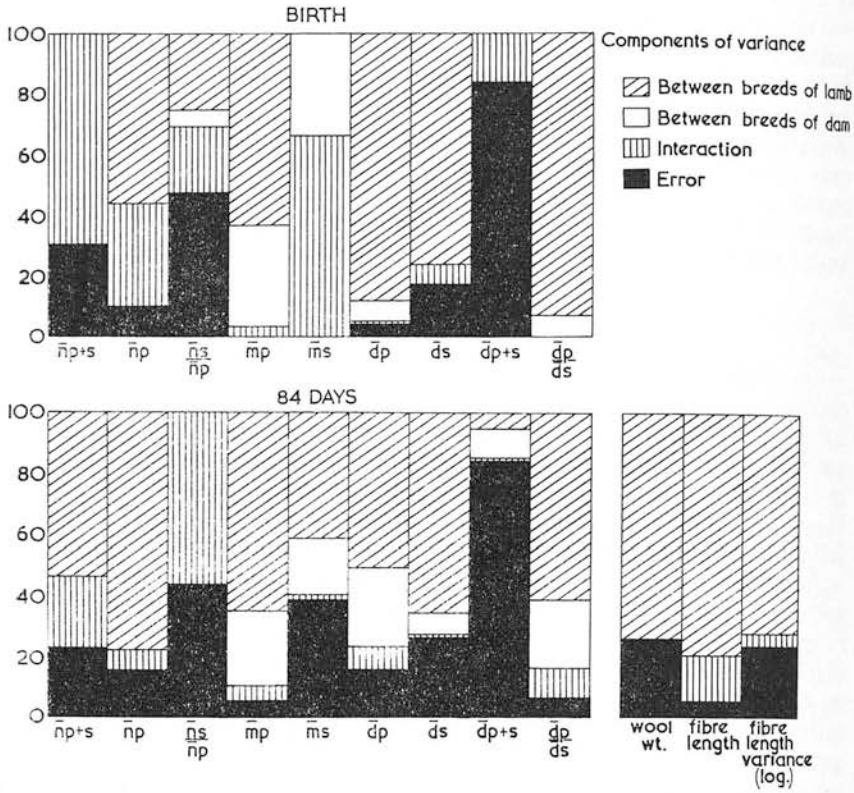

FIG. 1. Partitioning of variation in fleece and skin characteristics of Lincoln and Welsh Mountain lambs.

fleece samples taken at 84 days old from pure Lincoln and pure Welsh lambs born in the previous two years on the same farm as the animals in the present study and representing the flock from which the animals in the egg transfer experiment were a sample. Consideration of the additional data (6 Lincoln singles and 18 twins, and 7 Welsh singles and 22 twins) suggests that the small number of control lambs available in the present study has not produced misleading or unrepresentative results.

Follicle density. Generally, treatments causing a decrease in foetal growth rate are characterised by an increase in follicle density if the initiation of pelage follicles is not reduced in proportion to the surface area of the lamb. On the other hand, nutritional deprivation causing inhibition of follicle development will normally affect secondary follicles to a greater extent than primaries since the secondaries develop much later in gestation

when the foetus in most sensitive to nutritional treatments. If these two types of process occur together their effects may be confounded.

Particularly at birth, transferred Lincoln lambs had a reduced $\bar{n}_s/\bar{n}_p$ ratio, but also a reduced follicle density despite the fact that these lambs at birth were smaller in size than non-transfer Lincolns. The effects of reduced surface area alone would have increased density and the difference would have been expected to be in the opposite direction to that observed. It can be assumed therefore that there was a considerable physiological effect of the Welsh maternal environment which suppressed secondary follicle development in the transferred Lincoln lambs. By contrast the Lincoln maternal environment appeared to have no specific effect on follicle development in the transferred Welsh lambs since their $\bar{n}_s/\bar{n}_p$ ratio did not differ from that in non-transferred Welsh lambs, but their follicle density was lower, as expected from their slightly larger body size at birth.

The comparison of twins with singles among the non-transferred lambs showed that at birth and at 84 days old follicle density did not differ significantly but the trends were in the expected direction. The smaller animals —the twins—had the higher density. Whilst at birth there was a slight trend towards reduced secondary follicle development among twins (as shown by the $\bar{n}_s/\bar{n}_p$ ratio), this effect was more obvious at 84 days old and may indicate a predominantly post-natal disadvantage of lambs born and reared as twins relative to singles. This may be compared with a predominantly pre-natal effect following egg transfer.

Our results amplify those of Doney and Smith (1964), Schinckel (1953) and Schinckel and Short (1961) who all found that limitations in pre-natal nutrition caused a reduction in secondary follicle number and $\bar{n}_s/\bar{n}_p$ ratio. Doney and Smith were concerned with differences between single and twin lambs. They found that the effects were not permanent if post-natal nutrition was adequate—when, for example, twins were reared as singles. The effects in our Lincoln transfer lambs were, by contrast, longer lasting. This tends to support the view that the Welsh maternal environment was unfavourable for the Lincoln lambs, and certainly more limiting than the effects of twin pregnancy. It must be presumed that Ryder (1955) and Wildman (1958), who found no effects of pre-natal nutrition on the $\bar{n}_s/\bar{n}_p$ ratio, were dealing with even less severe nutritional deprivation or with breeds of sheep (Cheviots and Romneys) which reacted differently.

Wool production. Twelve weeks after birth, wool fibres on Lincoln lambs were twice as long as those on Welsh lambs. Probably most of this large difference would be caused by differential rates of fibre growth, but part of it may be due to fibre shedding in the Welsh lambs. This difference in fibre length was presumably the main cause of the genotypic difference in wool production (weight) since mean fibre diameter was the same in the two breeds. In addition to the genetic differences there were effects, the result of egg transfer, whereby both breeds of lamb had shorter fibres when born to and reared by their own breed of dam than they had in the transfer environments.

As shown earlier, Lincoln lambs in the Welsh environment had suffered a depression in secondary follicle density and yet showed virtually no depression in wool production. It seems likely, therefore, that these lambs compensated for their reduced number of secondary follicles by increasing fibre growth rate. Among the Welsh lambs the situation was slightly

different. Welsh lambs from Lincoln mothers showed no appreciable difference in the number of secondary follicles (as deduced from the $\bar{n}_s/\bar{n}_p$ ratio), but being slightly larger lambs, they showed a reduced density of all follicles presumably owing to the surface area effect. Therefore in the Lincoln transfer lambs and in the Welsh transfer lambs follicle densities were reduced for apparently different reasons, but the effect was the same, namely, an increase in fibre growth rate. These findings support the competition theory of follicle development put forward by Fraser (1951, 1952). They are also in line with the conclusions of Henderson (1953), Short (1955*a*, *b*), Schinckel (1957) and Schinckel and Short (1961) to the extent that pre-natal nutritional deprivation can permanently reduce the number of follicles formed, without impairing subsequent wool production. This is because the existing follicles can compensate by producing longer and coarser fibres if post-natal nutrition is adequate. In this sense, therefore, wool production per unit area of skin can be independent of follicle density. On the other hand, twins compared with singles had a lower wool weight at 84 days because fibre length had not made up for the reduced production of secondary follicles. This may be due to lack of time for compensatory fibre growth to occur by 84 days since the evidence in the twin situation pointed to post-natal rather than pre-natal nutritional deprivation.

SUMMARY

By mean of egg transfer, lambs of a large breed of sheep (Lincoln) were born out of dams of a small breed (Welsh Mountain) and vice versa. One breed was approximately twice the weight of the other. The effects of this contrast in maternal environment upon the development of the wool follicles and upon subsequent wool production are described in this paper. These effects are compared with differences between singles and twins.

Data were obtained from skin and wool samples taken at birth and at 84 days post-partum.

Genetic differences were the largest single source of variation for most of the component characters of the skin and fleece.

Strong maternal influences were in evidence. These were shown to have affected both Lincoln and Welsh lambs in a general (average) way and also to have had different, specific effects on each genotype as shown by genotype-environment interactions. Differences in maternal environment following egg transfer, clearly affected follicle density, primary/secondary follicle ratio, fibre medullation, fibre diameter and fibre length. Wool production was not affected, apparently because reduced follicle density was associated with increased fibre length.

In the comparison between singles and twins the latter appeared to suffer a post-natal rather than a pre-natal restriction of secondary follicle development, and in the absence of extra fibre growth there was reduced wool production at 84 days.

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A COMPARISON OF THE BODY SIZE, FLEECE WEIGHT AND MATERNAL PERFORMANCE OF FIVE BREEDS OF SHEEP KEPT IN ONE ENVIRONMENT

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THE purpose of this paper is to compare female sheep of five breeds (Scottish Blackface, Cheviot, Welsh Mountain, Lincoln Longwool and Southdown) which were maintained together as a single grassland flock. Particular interest in this situation is derived from the fact that breed differences are not confounded with differences of farm environment, at least from the age of six months when the sheep were brought together. In Great Britain, different breeds—and especially hill breeds—are, as a rule, kept in separate regions not merely on separate farms.

The sheep in this study represent the foundation population for a long-term experiment involving crossbreeding and inbreeding which was designed and, for the period covered by the present paper, carried out in collaboration with Dr. A. G. Dickinson and Dr. St. C. S. Taylor of the Animal Breeding Research Organisation.

MATERIAL AND METHODS

Female sheep were purchased as lambs in September 1955. At that time the Welsh Mountain sheep were five months old. Birth dates were not known for the Scottish Blackface and the Cheviot lambs but they were born during the lambing period normal for the district, which would make them the same age as the Welsh, viz. five months old. The Southdowns were, on average, about three weeks older and the Lincolns five weeks older.

In order to make the sheep as representative as possible of their respective breeds and to obtain, as far as possible, unrelated sheep for the experimental flock, the lambs of each breed were chosen from flocks which were large, using many rams and were 'typical' of their breeds. The Blackfaces and Cheviots were bought in open market and each breed was drawn from four sources, the Welsh were obtained from two flocks in Merionethshire (one belonging to the Animal Breeding Research Organisation), the Lincolns came from two flocks in Lincolnshire and the Southdowns from two flocks in Sussex. The Blackfaces represented an admixture of the Lanark and Newton Stewart strains. The Cheviots were the South Country type.

The sheep were brought together to Blythbank, Peeblesshire, a grassland farm at an elevation of around 800–1000 feet. They were run and managed as a single flock throughout their life. They grazed fenced fields and were moved between fields as management required. Supplementary feed (hay and concentrates) was offered only during periods of prolonged snow and for about six weeks prior to lambing. It was observed that all the breeds availed themselves of these supplements. Hardly any segregation of the

breeds was observed when they were first put together in the fields and none at all after a period of some weeks.

The females were first mated to lamb at about two years old. All were kept until $3\frac{1}{2}$ years old when they had had the opportunity to produce two crops of lambs. About half the females of the three hill breeds, all the Lincolns but no Southdowns were retained for a further year and a further lamb crop. No culling on performance took place, the females disposed of at $3\frac{1}{2}$ years being surplus to numbers required for subsequent experimentation.

The females of the three hill breeds were mated to two rams of each of the five breeds already mentioned and of a sixth, the Merino. Lincoln females were mated only to Lincoln or to Welsh Mountain rams, Southdown females only to Southdown rams. The pattern of mating in the first year (1956) and the number of females mated in each class are shown in Table 1.

TABLE 1

Mating pattern and numbers mated in first year

Breed of female	Breed of sire						Total
	B	C	W	L	S	M	
Scottish Blackface (B)	14	12	12	13	12	11	74
Cheviot (C)	12	14	13	11	12	12	74
Welsh Mountain (W)	12	12	14	10	11	11	70
Lincoln (L)	—	—	12	12	—	—	24
Southdown (S)	—	—	—	—	12	—	12
Merino (M)	—	—	—	—	—	—	—

The pattern in the second year was the same. In the third year, apart from some Welsh females mated to Lincoln rams, the Blackface, Cheviot and Welsh females were mated only to Blackface, Cheviot or Welsh rams, thus producing nine types of lamb (Table 1). The Lincoln females were mated, as before, to Lincoln or Welsh rams. Each female was mated to a different breed of ram every year. Two new purchased rams of each breed were used each year; they were all unrelated to each other.

Sheep were weighed to the nearest 1 lb. and the following eight body parts were measured to the nearest 0·1 cm.:

Body length—from the anterior point of the shoulder (tuberosity of the humerus) to the posterior extremity of the pin bone (tuber ischii).

Chest depth—the vertical plane passing through the highest point over the withers.

Shoulder width—the horizontal plane at the widest point over the infra-spinatus muscle.

Hook width—the extreme width of pelvis over the tuber coxae.

Pelvis length—from the anterior part of the tuber coxae to the posterior point of the tuber ischii.

Head width—maximum width at the supra-orbital processes.

Tibia length—measured on right hind-leg along the anterior surface.

Cannon bone length—measured on right fore-leg along the anterior surface.

Five observers were involved in the measurements. Analysis by Dr. St. C. S. Taylor showed that variation in subclass means was due to mean

differences between observers and to age × observer interactions. The data on linear body parts were statistically adjusted for mean observer differences and the results in this paper are based on these adjusted values.

Up to the age of 72 weeks weights were taken every two weeks and measurements every four; thereafter the frequency was three- and six-weekly respectively. The results presented for body size up to 174 weeks of age apply to sheep surviving this full period. Results for ages after 174 weeks (when only a proportion of the original stock were retained) apply to survivors to 232 weeks old (i.e., the last weighing and measuring prior to disposal).

RESULTS

Body size

Average live-weights for each breed of sheep are shown in Figure 1 for ages from approximately six months to 4½ years old. It is evident that for approximately the first year or 18 months after their arrival at Blythbank

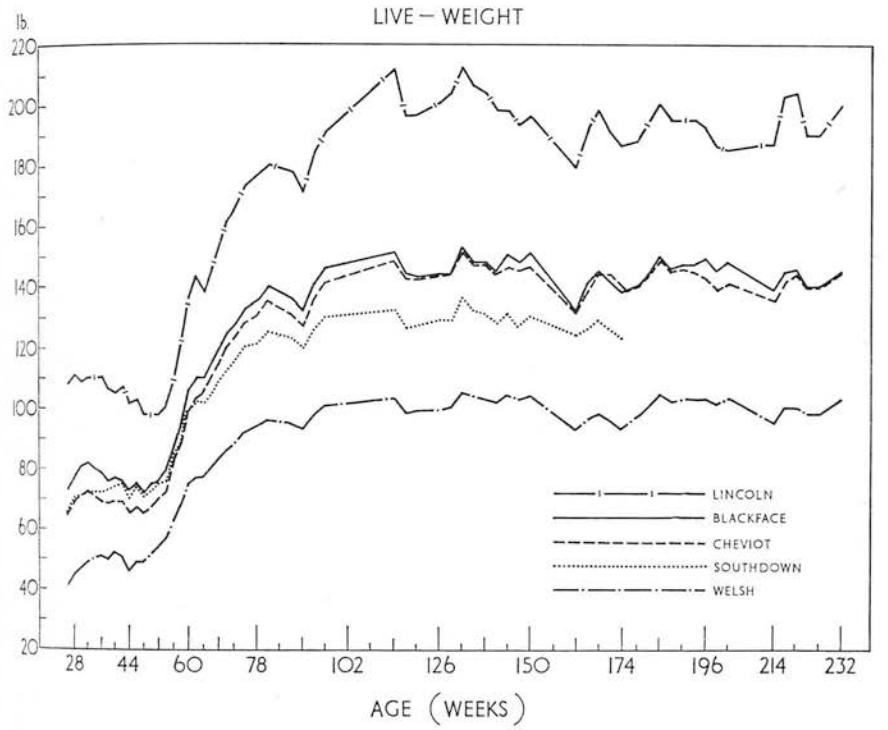

FIG. 1. Average live-weights of female sheep of five breeds at regular intervals from 26 to 232 weeks old.

the relative growth rate of the five breeds was not the same. For example, the weight ratio of the Lincoln and Welsh breed was 2·6:1 at the first weighing in October 1956, 1·7:1 in May of the following year (after the winter) and around 2:1 from about two years of age onward. At the start, the Blackfaces were significantly heavier ($P < 0{\cdot}001$) than the Cheviots but finished at about the same weight. On arrival, the Southdowns, were, on average, the same weight as the Cheviots but actually gained more weight over the autumn

and winter period than the latter and matured earlier and at a lower weight. This difference in the rate of maturity would seem to apply even if allowance were made for the three-week age difference between the Southdown and Cheviot females on arrival at Blythbank.

Figure 2 shows the corresponding values for eight body parts. Errors of measurement are likely to contribute to the minor fluctuations seen in the

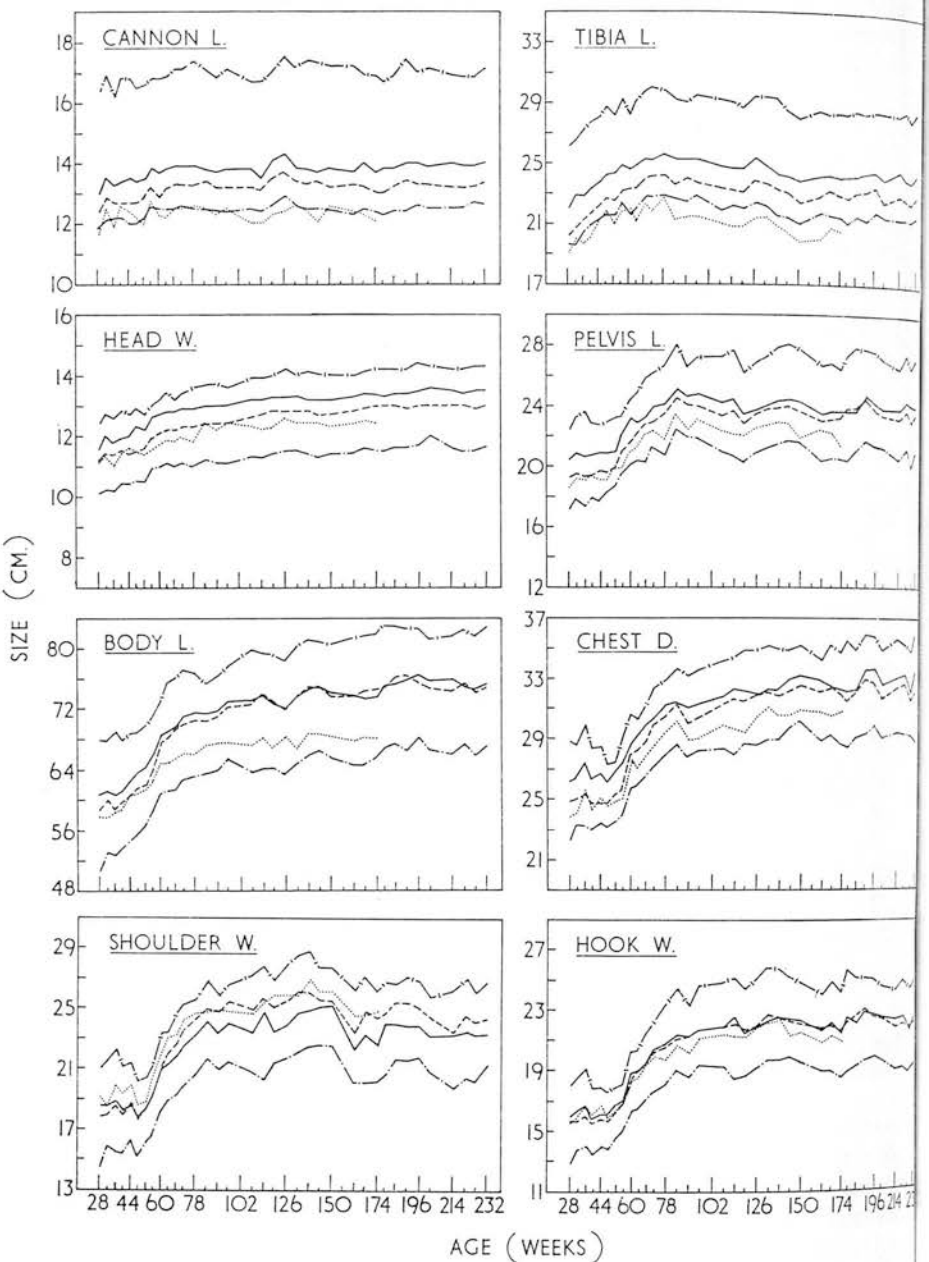

FIG. 2. Average size of eight body parts of female sheep of five breeds at regular intervals from 28 to 232 weeks old. Key to breeds as for Figure 1.

growth curves. Long-term trends, however, are unlikely to be so affected. From visual inspection it appears that some body parts such as shoulder width and hook width resembled live-weight in showing breed differences in their growth pattern whilst others such as tibia length and cannon bone length showed the breeds in close parallel. The ranking of body parts in terms of this overall agreement with live-weight is correlated almost completely ($R = 0{\cdot}98$) with the ranking of the body parts in order of earliness of maturing in relation to mature size (Figure 3). If breed differences in relative

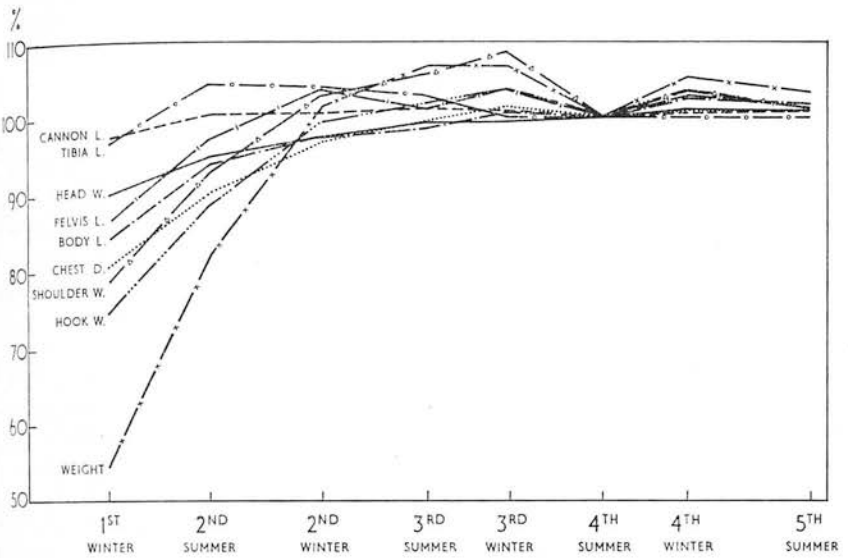

FIG. 3. Average live-weights and average sizes of each of eight body parts of female sheep at seven age-periods between 6 months and 4½ years old expressed as a percentage of the appropriate average size at 3¾ years old (summer 4). The age periods correspond roughly to winter and summer in each year of the sheep's life starting with the first winter (from 6 to 12 months) and ending at 4½ years old. The base period (summer 4) is shorter than average (162–174 weeks, i.e., the average of 6 weights and 3 measurements) and the following period (winter 4) correspondingly longer.

growth existed for the early maturing body parts such as tibia length and cannon bone length they must have been manifested before the age of about five months when the lambs were purchased.

The breeds did not differ in the order in which live-weight and the eight body parts reached mature size. Figure 3 shows the order for all the five breeds combined. Measurements averaged over periods of ages (in order to reduce fluctuations due to short-term changes and residual errors of measurement) have been expressed in terms of the size at age 162–174 weeks. It is obvious that live-weight and shoulder width and, to a lesser extent, several other body parts exceeded the size attained at the chosen age—which covers a period when these ewes were rearing their second lamb crop and were apparently in lean condition as a result of pregnancy and lactation. Since measurements of body parts on live animals are much affected by fat deposition and the thickness of other tissues the observed reductions in size do not imply any bone shrinkages. What small breed differences there were in degree of maturity reached by each body part at the age between six months and one

year showed the Cheviot to be generally the least mature and the Southdown and Blackface by-and-large to be the most mature. For example, the proportion of the 3¼-year old size reached between six months and one year was, for live-weight, Cheviot 50%, Blackface 56%, Southdown 58% and for tibia length 94%, 96% and 100% respectively.

There were appreciable differences between the breeds in conformation as shown by the fact that breeds did not rank in the same order of size for all body parts (Figure 2). For example, the Southdowns were the shortest of the breeds in the leg but nearly the widest at the shoulder, next only to the much heavier Lincoln. Blackfaces compared with the Cheviot were longer in the leg, narrower in the body—particularly at the shoulder—but of equal body length.

Variability in body size

Table 2 shows for the females surviving to 174 weeks old in each breed the average variance of live-weight and of the eight body parts at each of three periods of ages—26–72 weeks, 78–126 weeks and 132–174 weeks. Since between seven and twelve measuring occasions (and twice as many weighings) are included in each period, short-term fluctuations, including measuring errors, are unlikely to affect any long-term trends.

On average, the Lincoln breed appeared to be the most variable and was followed by the Blackface, with the Welsh and the Southdown being the least variable. Among the body parts there was highly significant agreement ($P < 0{\cdot}001$) in the ranking of the breeds for variability—the coefficient of concordance (W) being 0·67. In relation to the mean size of each measurement (the coefficient of variation) there was much less difference between the breeds. Concordance of ranking among body parts was small ($W = 0{\cdot}16$) and non-significant. There was a tendency for the ranking of the breeds on their coefficients of variation to be similar to the ranking of the breeds on their variances in respect of the late-maturing measurements such as live-weight, hook width and shoulder width but not in respect of the earlier maturing body parts. In Table 2, coefficients of variation are shown averaged over the five breeds for each period.

Age changes in variance are seen to be related to the earliness of maturity of the parts (Table 2). With increasing age the early-maturing parts tended to decline in variance while the later maturing body parts increased a little and live-weight increased 3½ fold (six-fold between 26 weeks and 174 weeks of age). Pelvic length decreased more in variance than its rank in the order of maturity would suggest. It can also be seen from Table 2 that most of the average changes in variance took place between the first and second age periods and, with the exception of live-weight (and cannon bone length to a smaller extent), very little further change took place between the second and third periods. The same general pattern emerges from the age changes in the coefficient of variation (see last column of Table 2). For all body measurements except live-weight the coefficient of variation declined slightly with age—that is to say mean size increased whilst variation either declined or increased proportionately less.

There were some minor, but interesting, breed differences in the age changes of variance. For example, the Cheviot sheep which, even to the eye, had appeared as a very uniform group relative to the Blackface after they were purchased, increased proportionately more in variance (except in tibia

length and chest depth) such that in period 2 they were closer in variance to the Blackface than they had been in period 1. This was particularly so for live-weight for which, in period 1, the Cheviot group was only 42% as

TABLE 2

Average variances and coefficients of variation for live-weight (lb.) and eight linear body dimensions (cm.) of female sheep surviving to 174 weeks old in three consecutive age periods of approximately one year's duration each (body parts arranged in the order of maturity shown in Figure 3)

Measurement	Age period†	Breed (and number) of females B (67)	C (63)	W (61)	L (21)	S (12)	Weighted breed average of percentage of variance at each age (age period 1 = 100)	Weighted breed average of coefficients of variation
Cannon bone length	1	0·55	0·40	0·52	0·63	0·47	100	5·34
	2	0·52	0·46	0·48	0·63	0·44	100	5·20
	3	0·48	0·40	0·45	0·52	0·26	89	4·91
Tibia length	1	1·69	1·49	1·36	1·70	1·78	100	5·40
	2	1·61	1·26	1·19	1·51	1·15	88	4·83
	3	1·61	1·39	0·96	1·47	1·27	86	4·92
Head width	1	0·26	0·18	0·16	0·22	0·13	100	3·78
	2	0·27	0·19	0·14	0·20	0·13	99	3·52
	3	0·29	0·18	0·14	0·18	0·11	98	3·45
Pelvic length	1	1·66	1·70	2·12	1·93	1·45	100	6·53
	2	1·40	1·62	1·42	2·20	1·51	87	5·30
	3	1·50	1·20	1·26	1·94	1·46	78	5·05
Body length	1	9·92	6·02	8·09	11·69	5·34	100	4·56
	2	9·31	8·29	9·56	10·67	5·60	113	4·28
	3	12·06	7·11	8·78	10·74	5·42	113	4·21
Chest depth	1	2·22	2·07	2·10	2·81	1·41	100	5·57
	2	2·62	2·32	2·08	2·28	2·34	110	4·99
	3	2·61	2·16	2·09	2·77	2·39	110	4·83
Shoulder width	1	1·87	1·62	1·48	2·98	1·54	100	6·91
	2	2·05	2·53	2·70	3·34	1·61	142	6·60
	3	2·56	2·52	2·21	4·16	2·74	148	6·68
Hook width	1	1·10	0·78	0·88	1·66	1·06	100	5·90
	2	1·36	1·11	1·18	2·10	1·49	133	5·42
	3	1·81	1·31	0·97	1·83	1·79	146	5·49
Live-weight	1	89·9	38·4	30·2	189·1	27·8	100	9·15
	2	164·4	139·0	78·4	425·7	96·0	267	8·96
	3	259·9	183·5	86·5	564·8	126·4	352	10·04

† Period 1, 26–72 weeks; Period 2, 78–126 weeks; Period 3, 132–174 weeks.

variable as the Blackface group but in period 2 this had changed to 85%. This is consistent with expectation on the basis of the somewhat slower rate at which the Cheviots reached their mature size (see earlier).

Fleece weight and wool shedding

Table 3 shows the average fleece weights for all females of each breed shorn in each of four years. In the first year, 1956, the females were about 15 months old at shearing. The fleece weights for that year were therefore

uncomplicated by any effects of pregnancy or of rearing lambs and, possibly because of the absence of these demands on the sheep, no wool was lost by shedding prior to shearing except for one Cheviot. It can be seen (Table 3) that at the first shearing there were large differences in average fleece weight between the breeds. The Lincoln breed produced about $2\frac{1}{2}$–3 times the weight of wool per sheep of the other breeds, but even when the Lincoln weights are excluded the breed differences were still highly significant ($P < 0{\cdot}001$). However, not all differences between any two breeds were significant.

TABLE 3

Average fleece weights (lb.) according to breed and year (all females)

		Blackface		Cheviot		Welsh		Lincoln		Southdow
Year	Shearing	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean S.
1956	1	5·30	0·10	5·06	0·09	3·88	0·03	13·04	0·27	5·13 0·
1957	2	7·04	0·17	6·42	0·21	4·71	0·11	16·64	0·77	6·26 0·
1958	3	5·22	0·19	4·27	0·25	3·49	0·13	12·77	0·41	4·63 0·
1959	4	5·66	0·28	4·29	0·34	3·48	0·17	13·04	0·47	— —

Prior to the next three shearings of the same females an appreciable proportion of the sheep had lost some of their wool by shedding it. The extent of shedding was assessed visually by Mr. E. Hughes (1956 and 1957) and Dr. J. Slee (1958 and 1959). Table 4 shows the total number of females at each shearing and the percentage which showed some shedding. In each year a significantly larger proportion of the Cheviot sheep than of the other

TABLE 4

The proportion of sheep shedding wool prior to shearing according to breed and year

		Blackface		Cheviot		Welsh		Lincoln		Southdow
Year	Shearing	No. ♀♀	Percentage shedding	No. ♀♀	Percentage shedding	No. ♀♀	Percentage shedding	No. ♀♀	Percentage shedding	No. ♀♀ Percen shedd
1956	1	74	0·0	74	1·4	70	0·0	24	0·0	12 0·
1957	2	71	4·2	70	21·4	68	4·4	24	4·2	12 0·
1958	3	67	44·8	63	69·8	60	53·3	22	4·5	12 0·
1959	4	34	58·8	35	88·6	36	69·4	20	10·0	— —
Totals and averages										
1957–9		172	30·8	168	53·6	164	36·6	66	6·1	(24 0·

breeds shed some wool. On average a slightly (but not significantly) larger proportion of the Welsh sheep than of the Blackfaces showed shedding: the Lincolns showed very little shedding and the Southdowns none at all. Among the sheep showing some shedding the amount of wool shed per sheep also differed between breeds with the Cheviot clearly shedding the most and the Welsh shedding slightly more than the Blackface (Dr. J. Slee, personal communication).

The number of lambs born per female was also associated with shedding (Table 5) such that the larger the number of lambs the greater the proportion of the females which had shed some of their wool prior to shearing ($P < 0{\cdot}001$).

A similar observation was made by Dr. J. Slee (personal communication) on sheep in a large hill flock of Blackface sheep. Prolificacy, however, can be only an additional factor to breed as a cause of the variation in shedding shown in Table 4, since the ranking of breeds for prolificacy is not the same as that for shedding (see later for reproductive performance).

Clearly, therefore, the fleece weights of the different breeds are differently affected by shedding. The fleece weights shown in Table 3 for shearings subsequent to the first are not therefore measures of wool growth alone, and any conclusions drawn from the breed differences in average fleece weight must take this into account. Among the three hill breeds the Blackface, although of similar body size to the Cheviot, clipped consistently and, after

TABLE 5

Fleece shedding, prior to clipping, in relation to number of lambs born per ewe (data from four breeds—Blackface, Cheviot, Welsh and Lincoln—and first three parities combined)

	No. of lambs per female			
	0	1	2	3
Number of females shorn	17	206	325	22
Percentage of females shedding wool	5·9	25·2	42·8	68·2

the first year, significantly more wool ($P < 0{\cdot}05$) than the Cheviot and the latter more than the Welsh. The Southdowns produced about the same average fleece weight as the Cheviots although smaller in body size—presumably because the Southdowns were unaffected by shedding.

Maternal performance

Breed type of the offspring may affect the number of lambs born per ewe, lamb survival and lamb weights. Hence the comparison of the five breeds of sheep in terms of their maternal performance was done in two ways –firstly, a comparison of the three hill breeds of ewe each mated to the six breeds of ram (i.e., producing purebred and crossbred progeny) and, secondly, a comparison of the five breeds of ewe each mated only to their own breed of ram (i.e., producing purebred progeny only). Lamb survival and weights were also analysed according to birth type and type of rearing.

Prolificacy and lamb survival. In each year a few ewes of each breed died in the interval between mating and lambing. No breed differences could be detected in this mortality possibly on account of the small numbers involved. Because of the effect of these deaths on the calculation of lambing percentage in relation to the numbers of ewes mated, the numbers of lambs born have been expressed as a proportion of the numbers of ewes lambing. The numbers of ewes which were mated but found to be barren during the lambing period are shown separately.

Lamb survival to weaning (at 15 weeks of age) is shown in place of the number of lambs weaned per ewe because a small amount of fostering and short periods of bottle feeding of lambs make a weaning percentage difficult to interpret. For example, ewes giving birth to triplets were not allowed to rear all three for experimental reasons which were unconnected with the

ewes' potential ability as mothers. In aggregate, over the three years, only nine lambs (1% of all lambs weaned) were not reared by their own breed of dam although 26 lambs (3%) were involved in fostering or in some measure of artificial rearing.

Survival of single-born lambs did not differ significantly from that of twin-born lambs in any year—in aggregate the percentages were 88·4 and 87·5 respectively—hence these two classes were pooled.

Table 6 shows the number of lambs per ewe and lamb survival classified according to whether the lambs were purebred or crossbred (further subdivided by breeds of sire). Differences associated with the breeding of the lambs were not significant.

TABLE 6

The average number of lambs born per ewe lambing in a flock of purebred Blackface, Cheviot and Welsh ewes and the proportion of lambs surviving to weaning according to breed type of lamb†

Year (and parity)	1957 (1)		1958 (2)		1959 (3)	
Type of lamb	Lambs per ewe	Lamb survival (%)	Lambs per ewe	Lamb survival (%)	Lambs per ewe	Lamb survival (%)
Purebred	1·61	91	1·82	84	1·88	85
Crossbred (from Blackface, Cheviot or Welsh sires)	1·43	89	1·82	78	1·94	84
Crossbred (from Lincoln, Merino or South-down sires)	1·45	91	1·77	85	—	—

† Differences in the number of lambs per ewe were significant between years ($P<0·05$) but not between types of lamb; differences in lamb survival were not significant.

Thus in these general terms the breed type of the progeny could also be ignored for purposes of the comparison of breeds of ewe shown in Table 7. It can be seen that, in each year, ewes of the Blackface breed gave birth to more lambs per ewe than the other breeds. The survival of their lambs was not significantly different from that of the other breeds. Among the three hill breeds, the Welsh ewes had the lowest number of lambs per ewe at birth but their lambs had, on average, the best survival ($P<0·05$). The breed difference in survival was apparently only partly accounted for by differences in numbers of lambs born per ewe since, as already pointed out, twins survived on average only slightly less well than single-born lambs. For example, the average difference in the survival of lambs born to Blackface and Welsh ewes was 2·5% for singles and 2·7% for twins.

Effects of live-weight. There was a superficial association between lambing performance and body size among the three hill breeds in as much as the Welsh breed was the smallest and had the lowest number of lambs per ewe. However, the association was not strong. The Lincoln, although twice the weight of the Welsh had very few more lambs per ewe than the latter and had a smaller number of lambs per ewe than either the Blackface or the Cheviot, both of which the Lincoln exceeded in size. Moreover, the Cheviot and

Blackface breeds differed very little in body size but significantly ($P < 0{\cdot}01$) in prolificacy.

There was a small difference in live-weight at the time of mating (November) between ewes which later (April–May) produced twins or triplets and those which gave birth to singles. On average (weighting the breed differences by the reciprocal of their sampling variances) the ewes with multiple births at first lambing weighed $2{\cdot}2 \pm 1{\cdot}4$ lb. more at the time of first mating than those producing singles. It is interesting to record that almost the whole of this difference in weight was already present at the age of six months, soon after

TABLE 7

The number of lambs born per ewe lambing for each of five breeds of ewe mated to several breeds of ram and the proportion of lambs surviving to weaning†

Year of lambing (parity)	Breed of ewe	No. of ewes lambing	No. of barren ewes‡	Lambs per ewe§	Lamb survival (%)
1957 (1)	Blackface	67	4	1·75	90
	Cheviot	71	2	1·46	89
	Welsh	67	3	1·22	91
	Lincoln	24	0	1·38	94
	Southdown	12	0	1·25	87
1958 (2)	Blackface	64	3	1·95	81
	Cheviot	66	0	1·86	79
	Welsh	66	1	1·58	88
	Lincoln	22	0	1·73	89
	Southdown	10	2	1·60	100
1959 (3)	Blackface	36	2	2·11	80
	Cheviot	36	0	1·89	82
	Welsh	30	0	1·73	94
	Lincoln	19	1	1·74	86

† For mating pattern in 1957 and 1958 see Table 1. 1959 data restricted to matings of Blackface, Cheviot and Welsh ewes with Blackface, Cheviot or Welsh rams, and Lincoln females with Lincoln or Welsh rams.

‡ Alive during lambing period.

§ Approximate standard errors for number of lambs born per ewe lambing in each class are as follows: Blackface, Cheviot, and Welsh in 1957 and 1958 $\pm 0{\cdot}06$, in 1959 $\pm 0{\cdot}09$; Lincoln and Southdown $\pm 0{\cdot}12$.

the females were purchased. Ewes having multiple births at the second lambing weighed $3{\cdot}8 \pm 1{\cdot}7$ lb. more at their preceding mating but at the third round they weighed $4{\cdot}7 \pm 2{\cdot}4$ lb. *less* ($5{\cdot}6 \pm 2{\cdot}5$ lb. less if the Lincolns are excluded). Although these differences are small the trends were the same for each breed (except that for the Lincoln the twin-producing ewes also weighed more on the third occasion). The ewes which were barren at lambing were not noticeably different in weight at the preceding mating from ewes which produced lambs. The small differences within breeds were not in a consistent direction.

Difficulties at birth. For all lambs born, whether live or still-born, a record was kept of whether parturition was normal or not and what degree of assistance, if any, was afforded. Interpretation of the results in terms of breed and other differences is complicated, however, by the excellent management which aimed at maximum survival. For example, at the first lambing

48% of the single lambs born to Welsh ewes were given 'slight' help during parturition compared with 25% for all other single-born lambs. Since the lambs included crosses with the Lincoln and other breeds larger in size than the Welsh, the difference may represent a 'real' breed difference in parturition difficulties, but it could also reflect some measure of anticipation of difficulties on the part of the highly efficient and conscientious shepherds.

Further, a record was kept of whether the lamb had to be helped to suck, was deserted by its dam, or was abnormal. The total number of lambs assisted in some form (parturition difficulties accounted for 68% of the total) represent those cases, therefore, where survival was presumably at greater-than-normal risk. Table 8 shows the number of still-births and the proportion

TABLE 8

The number of lambs born alive but assisted at or immediately after birth as a percentage of the total number of lambs in each class and the number of still-born lambs, according to breed of dam, birth type and parity

	Breed of dam											
	Blackface		Cheviot		Welsh		Lincoln		Southdown		All	
Type of birth†	s	m	s	m	s	m	s	m	s	m	s	m
Parity 1												
No. of lambs born	19	98	38	66	52	30	15	18	9	6	133	218
No. stillborn	—	5	2	1	2	1	—	1	—	—	4	8
% liveborn and assisted	37	19	42	14	52	17	33	11	44	68	44	18
Parities 2 & 3												
No. of lambs born	13	188	19	172	37	119	16	51	4	12	89	542
No. stillborn	—	11	1	9	2	2	—	2	—	—	3	24
% liveborn and assisted	31	10	16	21	19	15	6	29	50	17	19	17

† Single born = s, multiple-birth (twin or triplet) = m.

of live-born lambs assisted in relation to the total number of lambs born to each breed of ewe separately for parity 1, and for the two later parities combined (parities 2 and 3 did not differ from each other). The difference between first and later parities in the proportion assisted was highly significant in respect of single-born lambs ($P < 0{\cdot}001$) but was negligible for multiple births. Single-born lambs were helped into the world significantly more often than twins only in parity 1 ($P < 0{\cdot}001$). There were no significant differences among breeds of ewe in the proportion of their single-born lambs assisted in either first or later parities, but breeds of ewe appeared to differ in the amount of assistance afforded to their twin or triplet lambs (parity 1, $P < 0{\cdot}05$; parities 2 and 3, $P < 0{\cdot}001$). At later parities the breed difference appeared to be accounted for by the better performance of the Blackface breed compared with the others. The proportion of stillborn lambs did not differ materially among breeds of ewe, birth types or parities.

Lamb weights. Consideration has been restricted to single- and twin-born lambs at birth and to singles reared as singles and twins reared as twins by their own dam at weaning. Table 9 shows the performance of the three hill breeds of ewe when each was mated to rams from six breeds for the first

two lambings and to rams from three breeds for the last lambing. Essentially, therefore, each breed of ewe has given birth in any one year to lambs with the same average paternal inheritance.

There were no significant differences or consistent trends between the weights of offspring from matings with all breeds of ram (i.e., including the Lincoln, Merino and Southown) and the weights of lambs from matings confined to Blackface, Cheviot and Welsh rams in the two years (1957 and 1958) when this comparison was possible. This fortuitous circumstance has allowed a simplified presentation of the results. Thus a direct comparison between the performances in the three years (Table 9) is legitimate in spite of the change in average breed type of the lambs concerned.

TABLE 9

Average birth weights and weaning weights (with standard errors) of lambs born to Blackface, Cheviot and Welsh ewes mated to Blackface, Cheviot, Welsh, Lincoln, Merino and Southdown rams in 1957 *and* 1958 (*parities* 1 *and* 2) *and Blackface, Cheviot and Welsh rams in* 1959 (*parity* 3)†

Parity	Breed of ewe	Birth weight (lb.)				Weaning weight (lb.)			
		Singles		Twins		Single born and reared		Twin born and reared	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
1	Blackface	9·3	0·38	8·2	0·17	76·6	2·6	63·8	1·0
	Cheviot	9·9	0·33	8·3	0·17	73·1	1·4	59·1	1·4
	Welsh	8·7	0·17	6·9	0·18	62·5	1·2	50·2	1·5
2	Blackface	10·7	0·41	8·3	0·15	82·5	5·1	68·8	1·1
	Cheviot	10·3	0·43	8·2	0·13	78·5	4·6	60·4	1·1
	Welsh	8·8	0·21	6·5	0·09	67·1	2·1	53·6	0·9
3‡	Blackface	9·3	1·17	8·8	0·20	75·7	5·7	67·3	1·4
	Cheviot	10·5	0·74	8·7	0·20	77·7	3·3	64·6	1·5
	Welsh	9·7	0·39	7·1	0·17	71·4	2·6	55·4	1·4

† In parities 1 and 2, lambs of all breeds and crosses did not, on average, differ significantly in weight from lambs with Blackface, Cheviot and Welsh sires.

‡ N.B. Fewer crosses of lamb were represented in parity 3 than in parities 1 and 2 (see Table caption).

It can be seen that birth weights of single-born lambs increased slightly between first and second parity but that birth weights of twins stayed much the same. In the third parity there was an increase of about 0·5 lb. in the average birth weight of twins compared with parity 2. Weaning weights of lambs (at 15 weeks old) increased by about 4–5 lb. for singles after parity 1 and by about 3 lb. for twins from parity 1 to 2 and a further 2 lb. from parity 2 to 3.

There was little to choose between the birth weights of lambs born to Blackface and Cheviot ewes, but Blackface ewes weaned heavier lambs particularly twins (the one exception—single lambs from third parity Blackface ewes—is based on only three lambs). The Welsh ewes had lighter lambs both at birth and at weaning than the Blackface or Cheviot ewes but the difference in lamb weights was proportionately much smaller than the corresponding difference in live-weights of the breeds of ewe. This will be discussed later.

Table 10 shows the performance of each of the five breeds of ewe in the flock in terms of the weights of their purebred lambs alone. As such, their performance can be readily compared with the weights of purebred lambs born to these same breeds in other farm environments. In any direct comparisons in Table 10 among the breeds themselves, genetic and maternal effects are confounded. It can be seen that, as expected, Lincoln lambs were the heaviest at birth, but at weaning only their single lambs were appreciably heavier than those of any other breed whilst their twin lambs were only slightly, and not significantly, heavier than the pure Blackface twins.

TABLE 10

Average birth weights and weaning weights (with standard errors) of purebred lambs born to five breeds of ewe

Parity	Breed of ewe	Birth weight (lb.)				Weaning weight (lb.)			
		Singles		Twins		Single born and reared		Twin born and reared	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
1	Blackface	8·1	0·70	8·2	0·29	68·0	4·0	65·1	2·1
	Cheviot	9·6	1·32	8·9	0·27	67·0	1·2	62·9	1·5
	Welsh	8·1	0·26	6·7	0·28	58·3	1·5	48·7	3·2
	Lincoln	15·1	0·46	11·7	0·64	94·9	3·4	69·8	5·8
	Southdown	7·8	0·31	7·1	0·15	57·4	2·7	50·0	3·3
2	Blackface	(9·8)†		8·4	0·26	(82·0)		66·2	2·1
	Cheviot	(11·5)		7·9	0·25	(78·0)		60·6	1·6
	Welsh	8·5	0·32	6·9	0·19	57·0	5·1	49·4	2·1
	Lincoln	13·3	0·57	10·7	0·28	89·0	2·0	67·1	3·4
	Southdown	8·2	0·83	7·6	0·24	62·5	2·2	59·9	1·7
3	Blackface	(11·6)		9·4	0·31	(87·0)		71·4	2·8
	Cheviot	10·7	1·00	9·4	0·46	80·5	4·4	69·7	3·0
	Welsh	8·3	0·90	6·7	0·19	65·0	5·0	48·5	2·4
	Lincoln	14·2	0·90	12·0	0·30	93·3	5·9	72·0	1·3

† Figures in parenthesis are for single animals.

Comparison of Tables 9 and 10 shows that there was very little difference at either birth or weaning between the weights of the purebred lambs and the average weights of all lambs (including pure and crossbred) when Blackface or Cheviot ewes were the mothers (although purebred Cheviot twins were slightly heavier than the average of all lambs from Cheviot ewes). For Welsh ewes, purebred lambs were, with one exception, lighter at birth and in all six comparisons lighter at weaning than crossbred lambs.

DISCUSSION

The sheep of the five breeds in this study were maintained and managed as a single grassland flock and enjoyed equal opportunities from the age of 5–6 months on. Generalisations in terms of the relative merits of the breeds must, however, take account of the fact that breed differences are confounded with any differences in treatment up to the time the sheep were purchased. Such possible confounding effects may, however, have been lessened on average by each breed having been obtained from more than one source.

Account must also be taken of the possibility that the Blythbank environment favoured one breed more than another and that in a different environment this situation might be altered. Evidence for the importance of this kind of interaction in sheep is scanty. The most extensive studies derive from five strains of Australian Merino each kept at three environmentally quite different locations (Dunlop, 1962, 1963; Lax and Turner, 1965). These studies, covering a wide range of sheep production traits, showed that whilst statistically significant interactions were sometimes found to occur they were generally of moderate or small size and accounted for only a small fraction of the total variance. Osman and Bradford (1965) failed to obtain evidence of genotype-environment interaction with progeny groups of different rams kept in two distinct environments in California. Even in the more contrived situations where large environmental differences were created by different feeding levels and ambient temperatures, interactions between the breeds or strains involved and their environments were generally found to be small, but not necessarily non-significant, or absent (King and Young, 1955; King, Watson and Young, 1959; Morley, 1956). By contrast, the direct effects of different environments or treatments on the performance of sheep are generally large. Bowman (1966) in a recent review gives many references to the performance of sheep of different breeds and crosses in a large variety of situations. Particular attention will be drawn here only to the most relevant.

Blackface sheep of the same general type as those in the present experiment, but maintained under hill conditions on another farm belonging to the Animal Breeding Research Organisation and reported on by Purser and Roberts (1959), reached about two-thirds of the weight and had approximately half the number of lambs of the Blackfaces in the present experiment, as well as smaller lambs and lighter fleeces.

A flock of Blackfaces on the hill portion of Blythbank produced smaller adult sheep, less wool and fewer and smaller lambs per ewe (Donald, Read and Russell, 1963).

Differences for the pure breeds of up to 50% for live-weight and 100% for lambing percentage and big differences in lamb survival also arise out of the comparisons of the appropriate sheep at Blythbank with the Welsh sheep described by Purser and Young (1964)—the flock which provided the majority of the Welsh sheep for the present experiment—and by Dalton (1962), and with South Country Cheviots on a typical hill farm described by Gunn and Robinson (1963).

Thus, with reasonable evidence that, under a limited range of farm conditions, breed × environment interactions are likely to be small or negligible and with ample proof of the very large effects on performance of different environments some generalisations about the relative performance of the three hill breeds seem justified from the present results. The Blackface ewes grew a little faster, provided more wool, more lambs, and heavier lambs at weaning than the Cheviots and the Welsh. They also reached a final size greater (40% for live-weight) than the Welsh but not greater than the Cheviot. However, these differences do not necessarily reflect differences in overall economic merit since no assessment was made of feed consumption or differences in land utilisation. If live-weight could be taken to reflect these, then in relation to $(\text{weight})^{0.73}$ the Welsh produced less wool than the Blackface but, on average, about the same quantity as the Cheviot (presumably because less was shed by the Welsh prior to shearing). Further, per unit of metabolic

live-weight of ewe the lambing percentage of Welsh ewes exceeded that of Blackfaces at second and third parity and of Cheviots at all three lambings. Survival of lambs born to Welsh ewes was already better in absolute terms. Finally, per unit of metabolic live-weight of ewe the Welsh females produced heavier lambs at birth and at weaning than did either the Blackface or the Cheviot when the lambs included the crossbreds, but not when purebred lambs alone were considered.

One non-uniformity of treatment arose from the fact that Welsh ewes when crossed were mated to breeds of ram all larger than themselves whereas the two other hill breeds were crossed with rams of breeds both larger and smaller than themselves and the Lincoln ewes were crossed only with Welsh rams. Thus the scale of differences between the breeds of ewe in respect of lamb weights—though apparently not in respect of lambing percentage—has been affected by the choice of rams.

Crossbred lambs from Welsh ewes were on average heavier at birth (particularly for singles) and at weaning (for both singles and twins) than the purebred lambs. This suggests that Welsh ewes had the potential to bear and rear lambs genetically larger than purebred Welsh. In respect of the Blackface and Cheviot ewes the range of ram breeds used may not have put this point to the test, or the absence of differences in weight between purebred and crossbred offspring could indicate that a maximum of maternal capacity had been reached in these particular environmental circumstances. The latter alternative seems unlikely, however, from consideration of the cross with Lincoln rams alone since these crossbred offspring were heavier than average for Blackface mothers, although for Cheviot ewes the difference was absent at birth and not clear-cut at weaning. In general, however, the results support the view also derived from a consideration of Blackface, Welsh and Lincoln sheep in an egg-transfer experiment (Dickinson, Hancock, Hovell, Taylor and Wiener, 1962), that the limits of maternal capacity appear to be wide. Consideration of the magnitude of maternal effects affecting lamb size as estimated from reciprocal differences in this experiment will be given in a later paper.

Three findings of the present results show interesting differences from patterns reported by others. Survival of twins was in no year significantly different from that of singles. In the first year the small difference was actually in favour of the twins, possibly on account of the greater proportion of difficulties at birth among single-born lambs which may have affected their survival. Further, there was no apparent improvement in survival of singles or twins with increasing age of dam. Gunn and Robinson (1963) and Purser and Young (1964) have reported lower mortality for single-born lambs than for twins and better survival for lambs from older ewes than from first parity ewes in several hill flocks. Differences in environment and management of the sheep seem the most plausible explanation for the differences from present findings. Several studies (Reeve and Robertson, 1953; Coop and Hayman, 1962; Donald, Read and Russell, 1963; Purser, 1965; Bowman, 1966) show a positive association between litter size and weight of ewe. In the present experiment twin-producing ewes were heavier in the first two years, in conformity with the quoted reports, but lighter at the third mating by a significant 5·6 lb. if the Lincolns are excluded. Since ewes with twins in this flock—but not in some of the others referred to—were not separated from ewes with singles, the twin-rearing ewes may well be at a

relative disadvantage. Thus, in view of the large number of ewes which had twins both at second and third lambings, a positive genetic association between body size and subsequent lambing percentage may here be overshadowed by a negative environmental association, between lambing and rearing performance on the one side and subsequent body size on the other.

Consideration of the growth in weight and in linear body parts and of age changes in variance, particularly for the later maturing body parts, suggested that in relation to their mature sizes the Blackface and perhaps the Southdown breeds grew a little faster in the early stages than did the Cheviot. Some reserve must, however, be felt about this conclusion because birth dates were not accurately known for the Blackface and Cheviot groups and because of possible differences between the breeds in the treatment they received prior to purchase. Thus the breeds may have started the experiment at different stages of maturity for environmental reasons.

Age changes in variance of the different body parts were found to be related to the earliness of maturing of the parts. Variance of live-weight increased considerably, that of late-maturing linear parts by up to 50% between the averages of the first and third years, whilst that of some early-maturing parts decreased. There were some breed differences in variance particularly for weight, but in relation to mean size breed differences were not obvious. The coefficient of variation showed a slight decrease with age. There were breed differences in conformation but each body part had its own characteristic place in the order of maturity irrespective of breed.

Taylor (1962) and Taylor and Craig (1967) have shown as part of their detailed studies of the growth of twelve body parts in cattle that for monozygotic twins there was virtually no age trend in variance, but that, because mean size increased, there was a rapid decline in coefficients of variation. For dizygotic twins these authors have reported a continuous increase of variance with age and that the coefficients of variation remained more or less constant. This led to the conclusion that genetic variance within full-sib families increased with age. Monteiro and Falconer (1966) have reported for the weight of mice from birth to eight weeks old an increase in the phenotypic variance up to the age of five weeks followed by a decrease in spite of a continued increase in mean weight. The decrease in phenotypic variance was attributed to a decline in each of the two environmental components of variance but mainly to that between litters. Additive genetic variance continued to increase and, as with the cattle measurements (Taylor and Craig 1967), heritability estimates increased with age. If extrapolation to the present data, which are based on more or less unrelated sheep, is permissible and it is assumed that genetic variance continued to increase with age, the observed age changes in the variance reported for the sheep would be consistent with a, perhaps large, reduction in environmental variance with increasing age of the sheep. Some estimates of genetic and environmental changes in variances might have been made by presuming, from published data on sheep and cattle, the values of some of the likely heritabilities which might apply to the different body parts at various ages, but this seems unwarranted here because the contribution of measurement error to the sheep variances cannot be readily determined.

There are an appreciable number of published reports of body measurements in lambs in relation to differences in planes of nutrition and to carcass evaluation but few that provide relevant comparisons with the growth

patterns at the older ages studied here. Tallis, Turner and Brown (1964) have published coefficients of variation for a set of measurements of four linear dimensions on 40 Merino wether sheep at a single, unspecified age (assumed to be around 7 months old). Their coefficients are in general below those shown in Table 2. Greater accuracy of measurement of the Australian sheep probably accounts for the difference since each sheep was measured four times by the same observer compared with one measurement per sheep by any one of three observers at any age at Blythbank.

SUMMARY

Female sheep of five breeds (Scottish Blackface (B), South Country Cheviot (C), Welsh Mountain (W), Lincoln Longwool (L), and Southdown (S)) were purchased as lambs of 5–6 months old and subsequently kept as a single flock on a grassland farm until they were 4½ years old (Southdowns to 3½ years). The sheep were used in a crossbreeding experiment with up to six breeds of ram.

The sheep were weighed and 8 body parts measured at frequent and regular intervals. The Blackfaces and Southdowns grew, relative to their mature size, a little faster initially than the Cheviots. Mature weights (lb.) were approximately B: 146, C: 145, W: 101, L: 197 and S: 129. The breeds differed in conformation but the order of maturity of the body parts was the same for each breed. Variances for body measurements decreased slightly with increasing age for early-maturing parts and increased a little for later parts. The coefficients of variation decreased slightly with increasing age. Variance in weight increased markedly with age (but not the C.V.) and showed the only large breed differences in variance.

Fleece weight, after the first shearing, was strongly affected by the amount of wool shed prior to shearing. Shedding differed significantly between the breeds, Cheviots shedding most. Shedding was also related to the number of lambs born per ewe. The total weights (lb.) of wool produced from four shearings were B: 23·2, C: 20·0, W: 15·6, L: 55·5 and S (estimated from 3 shearings): 20·8.

The numbers of lambs born per ewe totalled over three lamb crops were B: 5·81, C: 5·21, W: 4·53, L: 4·85 and S (estimated from two crops): 4·55. In survival to weaning, single-born lambs were no better than twins and cross-bred lambs no better than purebred. Lambs born to Welsh mothers had the best survival; the other breeds did not differ significantly from each other. The breeds of ewe differed in the proportions of their twin lambs which had to be assisted at, or soon after, birth.

When each breed of ewe was mated to the same breeds of ram, the weights of lambs born to Blackface mothers did not differ significantly at birth from those of lambs born to Cheviots but were heavier at weaning. Lambs from Welsh mothers were the lightest at birth and weaning.

In relation to (live-weight)$^{0.73}$ the maternal performance of the Welsh females was at least as good as that of the Blackfaces but the wool production was slightly poorer.

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DENTAL OCCLUSION IN YOUNG BULLS OF DIFFERENT BREEDS

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SUMMARY

The position of the incisor teeth in relation to the maxillary pad was examined in bulls (at approximately 10 months old). Visual gradings grouped into five classes were made on 5582 bulls of eight breeds in the course of inspection for licensing. In addition, measurements of the tooth positions (grouped into 11 classes) were made on separate samples of 1163 Galloway and 191 Ayrshire bulls.

Among the beef breeds 84·0% of all tooth positions were classed as being normal and 96·6% of those among the dairy breeds. The proportion of mouths with incisor teeth forward of the maxillary pad was higher among the beef breeds. Individual breeds within the beef and dairy types also differed significantly.

Herds of the Galloway and of the Ayrshire breeds, judged on the bulls submitted for licensing, differed in the distributions of the position at which the incisor teeth met the pad. Herds also differed when judged on the occlusion of the sons of their bulls.

Heritability was calculated for Galloways by half-sib correlation and sire-son regression, yielding estimates from 0·31 to 1·28, suggesting that at least some of the variation is inherited. The undershot and overshot conditions were found together only rarely among the male offspring of any one bull.

INTRODUCTION

THE opportunity to study variation in dental occlusion in large numbers of cattle was presented by the records derived from bull licensing in Great Britain because the position of incisor teeth in relation to the maxillary pad is one of the factors considered. A licence can be refused if the central incisor teeth bite on the posterior half of the pad or fail to reach the pad (undershot), or if incisors extend beyond the pad to the extent that there is no contact between the upper part of the four central incisors and the front of the pad (overshot).

Much of the relevant literature dealing with jaw abnormalities was reviewed by Donald and Wiener (1954) who also provided data on occlusion for unselected calves and cows. The present paper is confined to information on bulls submitted for licensing (at about 10 months old) in the south-west of Scotland.

MATERIAL AND METHODS

The data are based on gradings of the position of the temporary incisor teeth in relation to the front of the maxillary pad in bulls aged about 10 months. Two sets of data were available.

1. Five thousand, five hundred and eighty-two bulls submitted for licensing for the years 1961 to 1967 were visually graded. Verbal descriptions varied from 'very slight' to 'bad' both for the undershot and overshot conditions. For purposes of analysis the data were grouped into five classes: 'normal' (when the cutting edges of the central incisors met the anterior angle of the pad), 'slightly undershot' or 'slightly overshot' (for any deviation prefixed by the inspector with the word 'slight') and 'undershot' or 'overshot' (for all other deviations).

2. One thousand, one hundred and sixty-three bulls of the Galloway breed and 191 Ayrshire bulls were examined in more detail by one of us (W. J. F. G.), with the permission of the farmers concerned, over a 10-year period ending in 1961. Verbal descriptions of gradings until 1954, grouped for analysis as above, were supplemented from 1954 onward by more detailed gradings, based on measurements with the 'normal' position designated 0 and each unit score representing a deviation of approximately 0·5 cm. A positive sign was ascribed to overshot and a negative sign to undershot conditions. Observations on the Ayrshire breed were confined to animals deviating from the 'normal'. The gradings were coded +4, +3, +2, +1, 0, −1, −2, −3, −4. Deviations in either direction of less than 1 were generally described as 'very slight' or 'zero+1' or 'zero—' and were scored as 0·5 for statistical analysis.

RESULTS

1. *Breed comparisons*

Table 1 shows the distribution of gradings for 5582 bulls classified by breed. It is clear that, except among the few Jerseys, a larger proportion of

TABLE 1

Frequency distribution of visual gradings of dental occlusion in young bulls of various breeds in south-west Scotland (1961–67)

	Total number	Percentage				
		Overshot	Slightly overshot	Normal	Slightly undershot	Undershot
Ayrshire	1805	0·1	1·7	96·3	1·8	0·1
British Friesian	1114	0	0·9	98·1	0·8	0·2
Dairy Shorthorn	351	1·1	3·7	94·6	0·6	0
Jersey	19	5·3	15·8	78·9	0	0
All dairy	3289	0·2	1·8	96·6	1·3	0·1
Aberdeen-Angus	90	3·3	10·0	85·6	1·1	0
Beef Shorthorn	126	1·6	8·7	88·9	0·8	0
Galloway	1242	2·4	5·8	88·4	2·9	0·5
Hereford	835	8·4	14·1	76·5	0·9	0·1
All beef	2293	4·6	9·1	84·0	2·0	0·3
All breeds	5582	2·0	4·8	91·4	1·6	0·2

bulls were graded as 'normal' among the dairy breeds (average 96·6%) than among the beef breeds (average 84·0%). Specifically, the bulls of the beef

breeds submitted for licensing differed from those of the dairy breeds in having a larger proportion classed as 'overshot'. The difference in the distribution of the grades between bulls of the dairy and beef types is highly significant statistically ($P \ll 0{\cdot}001$), but within the beef and dairy categories the differences among the breeds is also highly significant ($P \ll 0{\cdot}001$) even when the large contribution of the Jerseys to the total χ^2 value is discounted.

2. *Detailed observations on Galloway and Ayrshire bulls*

The detailed gradings on the Galloway yielded eleven classes in place of the five given above. The detailed gradings, when grouped into five categories as above did not show precisely the same distribution as the routine gradings shown in Table 1 (there were fewer normal, and in particular, more undershot), but the two sets cover different periods of time and the detailed work was also intended to record minor variations which might be classed as normal during the routine inspection. The detailed gradings, made by one observer, lend themselves, however, to a number of additional comparisons.

Herd differences

Herd comparisons for the Galloway include the proportion of bulls graded as normal, whereas for Ayrshire herds there is no record of normal bulls and comparisons are confined to testing for differences in the distribution of the various categories of malocclusion.

Galloway herds (excluding the smallest ones) were found to differ significantly ($P < 0{\cdot}05$) in the proportions of undershot and overshot bulls submitted for licensing. For the Ayrshire breed there was a corresponding significant difference only between the herd submitting the largest number of bulls (where the overshot condition was rare) and the rest of the herds combined (where the overshot and undershot condition was almost equally represented). However, such differences may arise for a number of reasons including any selection which may have been practised by the owners of the bulls.

Bulls submitted for licensing were classified according to the herds from which their sires originated. The comparison of herds based on the phenotypes of sons of their bulls (used mostly in other herds) is likely to reflect a greater proportion of any genetic differences among herds than the earlier comparison of the same herds on the basis of the bulls submitted by them for licensing. In the Galloway breed there was significant heterogeneity ($P < 0{\cdot}01$) among herds whose bulls were represented by 11 to 20 sons. The 18 herds whose bulls had left more than 20 sons gave a significant χ^2 value ($P < 0{\cdot}02$) only for a three-way classification into normal, undershot and overshot mouths. In the Ayrshire breed there was again a highly significant difference ($P \ll 0{\cdot}001$) between the largest bull-breeding herd and all the other herds combined. Relatively few of the sons of bulls from the large herd were overshot.

The herds with the greatest genetic influence on their breed are those which have provided the sires of many bulls and which themselves submit many bulls for licensing (cf. Wiener, 1953). The top ten Galloway herds (from among the 128 herd names appearing either among bulls or fathers of bulls) were picked on the basis of their numerical importance. They had provided the sires of half the bulls in the sample and had themselves submitted 30% of all the bulls for licensing. Twelve per cent of the bulls they

submitted for licensing were classed as having some deviation, however slight, from a 'normal occlusion', but 18% of the sons, mostly in other herds, were classed as 'deviant'. The top herds did not differ from each other in the proportion of normal to deviant bulls or in the proportions of undershot and overshot bulls. Judged by the next generation of bulls, however, these herds differed markedly in the proportions of their sons classed as having a deviant occlusion ($P \ll 0{\cdot}001$) and also in the proportions of undershot and overshot sons ($P < 0{\cdot}10 > 0{\cdot}05$).

Resemblances among relatives

Half-sib correlation. The 1163 Galloway bulls submitted for licensing in 87 herds were classified by sire, yielding 287 paternal half-sib families. The intra-sire half-sib correlation was computed from an analysis of variance of the gradings of the position of the teeth in relation to the pad on a linear scale with eleven classes (the central one being the 'normal'). The computed value of $0{\cdot}32 \pm 0{\cdot}04$ can be multiplied by 4 on the assumption that the half-sibs are a random sample to give an estimate of heritability (h^2) of 1·28 which is consistent with the postulate that all the variation was genetic. Most of the 287 sires had offspring in only one herd although approximately 50 sires had offspring in two herds. Statistical adjustment for herd differences did not, however, alter the estimate of h^2. One hundred and five of the sires were represented by only one offspring each. These contribute to between-sire variation but not to within-sire variation. Following their exclusion from the analysis, suggested on statistical grounds (cf. Robertson, 1962), the remaining 182 half-sib families (with at least 2 half-sibs in each) yielded an estimate of h^2 of 0·97 with a lower 95% confidence limit of 0·70.

Parent-offspring regression. In the sample of Galloway bulls, 53 of those seen in earlier years had a total of 165 sons submitted for licensing in later years. The regression of son's score on the score of his father was $0{\cdot}155 \pm 0{\cdot}046$ (using the linear scale of eleven classes of dental occlusion) and the correlation was +0·25. An estimate of heritability derived from twice the regression is 0·31, with 95% confidence limits for h^2 of 0·13 to 0·49.

Relationship of undershot and overshot conditions. In the 40 Galloway and 28 Ayrshire paternal half-sib families with two or more deviant bulls there was an excess, particularly obvious in the Ayrshire data, of families which were predominantly, or exclusively undershot or overshot compared with what would be expected by chance. In the majority of families with deviations in both directions the deviations were very slight. If the deviation in one direction was marked, a half-sib's deviation in the other direction would be small. There were only 2 Galloway half-sib families each with one markedly undershot (grade −3) and one markedly overshot (+2) bull, and none such among the Ayrshires. If malocclusion alone were inherited but not its direction, the positive and negative deviations among the progeny of a sire would tend to cancel each other.

DISCUSSION

The breed differences in dental occlusion shown in Table 1 provide one source of evidence for heritable variation. A greater incidence of overshot mouths in animals of the beef breeds than in animals of the dairy breeds reported here for bulls was also found by Donald and Wiener (1954) among

unselected cows and calves in two herds. Factors in the environment and management of bulls, however, may differ among breeds and might have contributed to average breed differences in dental occlusion. For example, the prolonged period of suckling customary for Galloway bulls is unlikely to be equalled in the management of many Ayrshire bulls. This could affect tooth position in relation to the maxillary pad. Wiener and Purser (1957) have shown for example, that the position of incisor teeth was affected in sheep by level of feeding, the highest plane producing a slight but significant forward shift of the teeth in relation to the pad. Selection by herd owners of the bulls they submit for licensing, from among those born, may also contribute to average breed differences in dental occlusion.

Evidence of such selection comes from the comparisons among the 'top ten' Galloway breeders referred to earlier. They submitted a smaller proportion of deviant bulls than the breeders who used their bulls. Moreover, these herds when compared on the bulls submitted by them for licensing did not differ significantly in the average position of the incisors in relation to the pad or in the distributions of the positions. By contrast, they differed markedly when compared on the next male generation sired by their bulls. Clearly not all herd owners select their bulls before licensing since a number of markedly deviant mouths were seen during inspection. The significant differences found to occur among breeds within the dairy and within the beef categories may be less prone to confounding effects of selection or management.

For the Galloway bulls, the estimates of the heritability of the dental occlusion score (based on linear measurements) from half-sib correlation and parent-offspring regression were not in good agreement. The former suggested almost complete inheritance and the latter a moderate degree only. Bulls which became the sires of the next generation of bulls submitted for licensing represent a selected group since most of the extremes are not licensed for use. This is likely to have a greater effect on the accuracy of the estimate of h^2 based on half-sib correlation (1·28) than on the estimate based on parent-offspring regression (0·31). The half-sib estimate in particular may also have been affected by any selection of bulls before they were submitted for licensing. The half-sib estimate may further have been affected because the identity of dams of bulls was ignored though some of them may have had more than one son in the sample.

In the calculation of the parent-offspring regression it was found that the variance for sires was unexpectedly (and significantly) larger than that for sons. It is possible therefore that twice the parent-offspring regression underestimates the heritability (i.e. 0·31) and that twice the parent-offspring correlation provides a more accurate estimate (0·50).

Whichever estimate is preferred as an approach to the biological truth it seems evident that at least a moderate proportion of the variation in dental occlusion among Galloway bulls is inherited. Evidence of inherited variation for this trait was reviewed by Donald and Wiener (1954). Some more recent reports also demonstrate or postulate that inheritance is important, although the conditions studied qualify more as abnormalities than does the variation under investigation here. A paper by Grant (1956) reports on underdeveloped mandible in a herd of Dairy Shorthorn cattle which resulted in the death of the calves. Gregory, Koch and Swiger (1962) described malocclusion to the extent that the incisors extended forward of the dental pad by one-half to

three-quarters of an inch in a closed line of Hereford cattle. Meyer and Becker (1967) report an anomaly in which the incisors were forward of the maxillary pad and which affected 23 out of 47 calves on one farm. The affected calves were all offspring of one bull which also left such offspring in other herds, but, interestingly, the condition improved with age and had disappeared entirely by one year of age.

The inheritance of malocclusion has been attributed by some authors to a simple dominant, and by others to a simple recessive gene. Evidence from the offspring of particular sires in the present study would not be inconsistent with either postulate. The evidence, however, also points to continuous variation and the additive action of several pairs of genes. The observations provide good evidence that what is inherited is not only a predisposition to deviate from the normal but a directional deviation, i.e. an undershot or an overshot condition, but not both, with the possible exception of the very slight deviations.

It remains a matter for speculation whether maxillary or mandibular development, or both, are involved in producing malocclusion within the range recorded here. It may be that the answers will even be found to differ according to the past aims of breeders in relation to the conformation they have chosen for their animals.

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Factors Involved in Middle Ear Infection (Otitis Media) in Lambs

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SUMMARY.—In an experimental flock of sheep, over a five-year period, *otitis media* was found in 15 (2.97 per cent.) of 505 lambs which died between birth and eight months old and were examined *post-mortem*. The condition was not found in lambs under two days old. The 10 cases in lambs 3-42 days old represented 10 per cent. of those dying at that age. Among factors of breed and management examined, the occurrence of otitis media was particularly associated with bottle feeding, being found in nine of the 32 bottle-fed lambs.

Introduction

EXPERIENCE of lamb autopsies at the Veterinary Investigation Centre, Edinburgh, suggests that middle ear infections in young lambs are rare, although they have been found associated with generalised pyogenic infections such as "navel ill."

In the course of autopsies carried out on 505 of the lambs which died over a five-year period (1966-1970) in a grassland flock of experimental sheep at Blythbank in Peeblesshire, 15 cases of otitis media were found (2.97 per cent.). The purpose of this communication is to record the occurrence of the condition, the gross pathology and bacteriology, and the factors of breed and management which were involved.

Materials and Methods

Full details of the grassland flock and its management have been given by Wiener (1966). Briefly, the experimental flock comprised Scottish Blackface, South Country Cheviot, and Welsh Mountain breeds of sheep and the crosses among these breeds. Additionally, each of the breeds and crossbreeds was maintained at varying levels of inbreeding from 0-60 per cent. The inbreeding (parent-offspring or full sib mating for successive generations) had reduced birth weight, growth rate and survival of lambs. Up to weaning (15 weeks), mortality was 23.4 per cent.; prior to any inbreeding, the average pre-weaning mortality was 14 per cent. (Wiener, 1967). In the present study, the 550 lambs which died up to eight months old (including stillbirths) represented 26 per cent. of those born.

Single- and twin-born lambs were reared by their own mothers whenever possible. Ewes with triplets, of which there were few, had one lamb removed for fostering or bottle feeding. Lambs whose mothers had died or were unable to provide for them were suckled by a foster mother if available; otherwise they were fed on the bottle.

The 45 lambs (8 per cent. of the total) which died but were not examined *post-mortem* can be regarded as a random sample of those which died. Failure to send them for *post-mortem* examination arose only from difficulties of transport.

The tympanitic cavity of all lambs coming to autopsy was exposed by incision through the ventral wall of the osseous bulla of the petrous temporal bone. Routine bacteriological cultures were made from the contents. Paraffin sections were prepared from all the major anatomical divisions of the CNS, but the technical complexity of processing the petrous temporal as a routine, precluded histological examination of the ears.

The factors which were examined for their relationship to the incidence of lamb deaths in general, and to the incidence of middle ear infection in particular, were for the lamb: year of birth, breed, sex, birth type, type of rearing, the week of birth in the lambing period (April to early June) age at death, and inbreeding; and for the ewe: parity and inbreeding.

Results

Description of the Condition

Otitis media was found in 15 lambs; in 11 it was unilateral and in four bilateral. The condition was characterised by the presence of creamy-yellow purulent material within the bulla tympanica. The pus was frequently inspissated and extended a variable distance into the Eustachian tube. In all cases the ossicles appeared normal, the tympanic membrane was intact and otitis externa was not apparent on visual examination of the ear canal. Central nervous disturbances were not recorded in the *ante-mortem* histories of affected lambs, and histological examination of the CNS did not reveal any specific abnormalities.

Bacteriological examination of pus from the middle ear revealed *Pasteurella haemolytica* (12 cases), *Neisseria catarrhalis* (1), coagulase positive haemolytic Staphylococci (1), and mixed haemolytic Staphylococci and haemolytic Streptococci (1).

Associated Disease Conditions

The primary cause of death in five cases was attributed to pneumonia in four of which *P. haemolytica* was involved. Five further deaths were attributed to generalised weakness, two to helminthiasis and

one each to pulmonary abscess, and digestive disturbance. Pneumonias and digestive disorders were also among the more common secondary factors associated with death. In one case, an ill-thriven lamb which died at 14 weeks of age, otitis media (although associated with pharyngeal oedema and slight pneumonia) was considered to be a major factor contributing to death.

Factors Arising in the Flock

On the basis of the statistical criteria the year of birth, breed, sex, type of birth (single, twin or triplet), the degree of inbreeding of the lamb, and the parity and inbreeding of the ewe, had no apparent effect on the incidence of otitis media. On average its incidence was significantly greater among late-born lambs (8.3 per cent.) than among those born in the first four weeks (2.1 per cent.) but within years there was no consistent trend.

Deaths were classified in seven age groups. Table I shows the age distribution of deaths, and, for each age, the proportion with otitis media. The highest incidence (10 per cent.) was among lambs dying between three and 42 days after birth. No cases were found among stillborn lambs or those dying on the day of birth. The variation in the incidence of otitis media at different ages is highly significant ($P<0.001$) and remains significant ($P<0.02$) if it is assumed that otitis media is acquired after birth, and stillbirths are excluded from consideration.

The type of rearing appears to have been the single most significant factor in relation to the incidence of otitis media (Table II). Twenty-eight per cent. of bottle-fed lambs which died had middle ear infections ($P<0.001$) compared with 1.3 per cent.

TABLE I
AGE DISTRIBUTION OF DEATHS AND THE INCIDENCE OF OTITIS MEDIA AT EACH AGE AMONG LAMBS WHICH WERE GIVEN A POST-MORTEM EXAMINATION*

Age at death	No.	per cent. of total	per cent. of No. at each age with otitis media
Stillborn	148	29·3	0
Less than one day	105	20·8	0
1 or 2 days	69	13·7	2·9‡
3 to 7 days	48	9·5	10·4
8 to 42 days	50	9·9	10·0
43 to 105 days†	31	6·1	3·2
106 to 240 days	54	10·7	3·7§

*92 per cent. of lambs dying were examined *post-mortem*.
†Weaning took place at $105 \pm 3\frac{1}{2}$ days.
‡The two lambs with otitis media in this group were both two days old.
§The two lambs with otitis media in this group were 114 and 122 days old respectively at the time of death.

TABLE II
TYPE OF REARING OF LAMBS WHICH DIED (EXCLUDING STILLBIRTHS) AND THE INCIDENCE OF OTITIS MEDIA FOR EACH TYPE

	No.	per cent. of total	per cent. of No. in each class with otitis media
Reared by own dam	302	84·6	1·3
Fostered	23	6·4	8·7
Bottle-fed	32	9·0	28·1

of lambs reared by their own mothers and 8.7 per cent. of those fostered.

Age at death, however, was associated with the type of rearing. Among the dead lambs examined 71 per cent. of those bottle-fed had died within seven days of birth and all within 42 days, compared with 46 per cent. and 62 per cent. respectively for the suckled lambs (excluding stillbirths).

On the basis of birth weight the dead, bottle-fed lambs could not be distinguished from dead lambs which had been suckled, in spite of the greater proportion of twins and triplets (77 per cent.) among the bottle-fed lambs compared with all dead lambs (57 per cent.).

Also, among the dead lambs, those with otitis media had the same average birth weight as unaffected lambs. Eight of the lambs with otitis media had been born as singles, five as twins and two as triplets.

Discussion

The purpose of this paper is to draw attention to the occurrence of otitis media, a condition which does not appear to have been reported in lambs hitherto. The disorder was subclinical in the sense that neither neurological nor locomotor defects were noted in life, otitis media presenting itself as an incidental *post-mortem* finding. On the basis of the present evidence, the condition was acquired after birth and was associated with bottle feeding. However, the small number of lambs involved precluded a simultaneous analysis of all the relevant factors. In the special circumstances of this experimental flock it is difficult to extrapolate from the present results, but the problem seems to merit further investigation in the context of intensive systems of rearing in which large-scale bottle feeding, or its equivalent, is necessary.

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Résumé

Sur une période de cinq ans, on a enregistré dans un troupeau expérimental de moutons, 15 (2.97 pour cent.) cas *d'otites moyennes* sur un total de 505 agneaux. Les animaux en question sont morts avant d'avoir atteint l'âge de 8 mois et ont été autopsiés. Aucun agneau âgé de moins de 2 jours n'a été atteint. Les dix cas enregistrés parmi des agneaux âgés de 3 à 42 jours ont représenté 10 pour cent. des agneaux morts à cet âge. Les facteurs de race et de type d'élevage ayant été examinés, on a pu particulièrement associer ces cas d'otites moyennes à l'alimentation à la bouteille, 9 des 32 agneaux alimentés à la bouteille ayant été contaminés.

Zusammenfassung

In einem zu Versuchszwecken gehaltenen Schafbestand wurde im Verlauf von fünf Jahren bei 15 (2,97 pro zent.) von 505 Lämmern, die zwischen der Geburt und einem Alter von acht Monaten starben, beim Sezieren Mittelohrentzüundung festgestellt. Bei Lämmern, die weniger als zwei Tage alt waren, wurde diese Krankheit nicht gefunden. Die zehn Fälle bei 3-42 Tage alten Lämmern repräsentierten 10 pro zent der in diesem Alter gestorbenen Tiere. Bei der Untersuchung der einzelnen Züchtungs und Betriebsführungsfaktoren stellte sich heraus, dass ein besonderer Zusammenhang zwischen Mittelohrentzündung und Aufziehen mit der Flasche bestand. Neun von den mit der Flasche aufgezogenen 32 Lämmern litten an der Krankheit.

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Breeding for Increased Productivity

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PRODUCTIVITY in the sheep industry has many components and encompasses a diversity of environments and market products. Diversity of opinion is likely, therefore, on what changes would constitute improvement. The scope for improvement through breeding is considerable both on a national basis and in collaborative schemes among groups of farmers. Individually, most flocks are too small and exist for too short a time to make ambitious breeding schemes worth while. Even the smallest flock, however, requires some breeding decisions, be it the breed to be kept, to breed pure or to cross, what rams to use, which ewes to keep, and what traits to consider.

The present article outlines the options open for genetic change and suggests the more rewarding directions to follow. The broad issues of decision making involved on an individual or national scale in " breeding for increased productivity " have been given full consideration by Lerner and Donald (1966) and a lucid account of underlying genetic theory is given by Falconer (1960).

Methods of Change

The Use of Different Breeds

Breeds vary greatly in their attributes. The most rapid way of changing the performance of a flock is to change the breed.

A difficulty in assessing the genetic merit of different breeds arises from the fact that they are only rarely kept together under the same conditions. The point is illustrated in Table I. The left-hand side of the Table shows the average performance of the Scottish Blackface, the (South Country) Cheviot and the Welsh Mountain breeds when all three were run together as a single flock on a grassland farm in Peeblesshire. The right-hand side shows the same three breeds but each on a different hill farm (two belonging to the Animal Breeding Research Organisation and one to the Hill Farming Research Organisation). As expected, average bodyweight, fleece weight and lamb production were lower in each case under hill conditions, but the important point is that comparison of the three breeds on the right-hand side of Table I would lead to the assumption that Cheviot sheep were the heaviest breed with the heaviest fleeces and that Welsh sheep produced more lambs than either of the other two. But because each breed was kept, as is commonly the case, in a separate flock and a different environment, it is impossible to decide what is due to the effects of genes and what to the effects of environment. When the three breeds were kept together in one flock they showed a different order of merit, and differences can validly be attributed to the capabilities of the breeds kept in these conditions.

Similar considerations apply to *differences among flocks* within a breed. In many instances it would be less misleading to assume that flock differences in performance are largely non-genetic than to assume otherwise (Wiener, 1966). Genetic differences are less than might be supposed because farmers purchase breeding stock from each other and ultimately from a few flocks in each breed only (Wiener, 1961). Flock management and environment create large differences in performance and must not be ignored simply because the factors are not always readily definable.

It is often claimed that breeds are adapted to particular environments implying that *genotype-environment interactions* are important. For the relatively limited range of conditions in Great Britain there is little experimental evidence to substantiate the claim. In considerations involving disease, however, interactions may well be important and their relevance may be greater as the conditions under which sheep are kept polarise to greater extremes, each with particular stresses for the sheep, from the highly intensive systems to the remote impoverished grazings where sheep may have to fend for themselves.

TABLE I
AVERAGE PRODUCTION OF FEMALE SHEEP OF THREE HILL BREEDS

Breed	Grassland farm*			Hill farm			Source of data
	Mature liveweight (kg.)	Fleece weight† (kg.)	Lambs weaned/ 100♀♀‡ mated	Mature live weight (kg.)	Fleece weight† (kg.)	Lambs weaned/ 100♀♀‡ mated	
Scottish Blackface	67	2·6	151	41	1·7	81	ABRO
Cheviot (S.C.)	67	2·3	137	53	2·1	71	HFRO
Welsh Mountain	47	1·8	134	34	1·1	105	ABRO

*Adapted from Wiener, 1967, *Anim. Prod.* **9.** 177
†Average of first four shearings. ‡Average of first three lamb crops

Cross-breeding

Cross-breeding is well established in the British sheep industry. Geneticists advocate the use of specialised sire and dam lines to bring together in the offspring different desirable attributes from the two parents. The breeder recognises as a practical example of this the combination of the good maternal performance of hill breeds with the extra size derived from rams of, for example, "Longwool" breeds. Cross-breeding is also part of the stock-in-trade in evolving new "breeds" or "hybrid" types.

The first expectation is that the crossbred will be intermediate in performance between the levels of the parental breeds. Anything better than this average, usually referred to as hybrid vigour, can be expected as a bonus for only some traits, but important ones particularly those associated with reproduction and survival. Some advantages of cross-breeding, therefore, arise from using cross-bred females as mothers. Specific breed combinations sometimes are better and occasionally worse than expected, and unfortunately there is no short cut to finding out.

Cross-breeding could, with advantage, be used even more widely than at present. The commonly held view is that cross-breeding, on a national scale, requires large pure-bred populations to support it as, for example, the hill breeds basic to the present stratified breeding system. Self-replenishing cross-bred female populations can, however, be maintained by criss-crossing or by the rotational use of three or more breeds of ram. Only relatively small pure-bred populations are then needed to provide rams. There is also no genetic reason why cross-breds should not be mated to cross-breds. As much as half of any hybrid vigour contributing to the performance of the first cross may be lost, but in absolute terms this could amount to very little. Also, the marked uniformity of the first cross might not be repeated in a few outwardly visible trademarks such as facial colour, horns or fleece type; but in terms of the economically useful characteristics, increased variability is unlikely to be either a problem or even to be apparent.

In-breeding

In-breeding as a means of producing pure-breeding strains of highly meritorious sheep is almost certainly doomed to failure because most traits are affected by many genes, and unfavourable genes are as likely to become "fixed" in a homozygous state as favourable ones—indeed heterozygosity itself may be the more desirable state. In practice, in-breeding is accompanied by loss of vigour, high mortality, poor reproduction, and poor growth. But because some deleterious genes are lost through the death or culling of their in-bred "owners," crossing of selected, surviving lines of in-bred sheep may lead to marked improvements. Though this has been practised successfully with plants and with rapidly reproducing species like poultry, the costs in sheep would most likely outweigh any ultimate advantages —certainly for the individual breeder. Some future geneticist may answer differently if, through a study of biochemical pathways, the specific action of genes became recognizable in the components of important physiological or biochemical attributes of sheep.

Rams intended to be used widely, for example through A.I., if also suspected of carrying a major genetic defect, can be tested by mating them to a relatively small number of their daughters. This special case, however, does not justify any wider adoption of in-breeding.

Selection

The choice of superior individuals as the parents of the next generation is ultimately the most constructive way of creating lasting change, but it can be slow and expensive. Progress depends on the variability of the trait being considered and on the proportion of this variation which is inherited (heritability), on the superiority of the individuals selected relative to the group from which they were chosen (selection intensity), on the speed with which generations can succeed each other (generation interval) and thereafter, of course, progress depends on the scale and duration of the operation.

The recognition of superior individuals is basic to success; recording of performance is, therefore, essential. For many traits of economic importance the performance of an individual gives insufficient information about its breeding value and hence the need to resort to testing of progeny and of relatives. This increased accuracy of selection is bought, however, at the cost of a slower generation turnover and the right balance needs to be struck. Many of the necessary considerations and methods, such as, for example, the adjustments needed to make twins comparable with singles, are well set out in a 10-year-old but still highly pertinent publication on sheep recording and progeny testing (Min. of Ag., 1961).

The larger the number of traits being selected the less the attention that can be paid to any one of them. It is, therefore, desirable to keep objectives simple. For schemes involving more than one trait different procedures are possible such as consideration of one trait at a time in successive generations, regard to a specific level of performance separately for each trait but all at the same time, or selecting on an index which is constructed to give appropriate weight to each trait according to genetic and economic considerations. In theory an index is never inferior to the alternatives, but in practice it is likely to be more complicated and costly to operate (see Turner & Young, 1969). Bereft of their statistical refinements, so necessary to a large-scale breeding operation, the ideas must be familiar to any farmer faced with a choice of animals for breeding, none of which is "perfect" for any of several desired qualities.

Performance Traits of Sheep

Some of the traits with economic implications will now be considered separately although, clearly, they are inter-related. No sheep, breed, or cross is likely to be good, never mind "best," in all respects *and*

(*continued on page* 611)

it should not be the aim of any breeding system to achieve this end. What emphasis to place on any one attribute, or a small combination of them, is the first decision needed. This point will be referred to again later. Many of the breeding experiments related to increasing meat production from sheep were reviewed by Bowman (1966).

Reproductive Performance

The number of lambs weaned per ewe mated, the "end" point in many commercial situations, can be regarded as comprising the number of lambs born, the number surviving, and the number of barren ewes in the flock. For intensively-managed flocks earliness and frequency of breeding must be included in flock performance. Although the component traits are weakly inherited, the selection which can be applied is quite high. For example, the use of twin- or triplet-born rams would place the selected group well above the average in most flocks. Purser (1969) has calculated that lambing percentage could be increased by one per cent. per year (a rate achieved in an experimental Romney flock in New Zealand) and that if practised in all breeds would result in an increase of 2.5 thousand tons in carcase meat each year. Turner (1969), in a pertinent review article, is more optimistic and claims three per cent. as a reasonable expectation for an annual increase. Geneticists are likely to agree, however, that any preference for the use of single-born rams (or ewes) —which may exist on account of their better looks, as lambs, compared with twins or triplets—can do nothing but harm to the cause of increasing natural fecundity.

Among breeds there is undoubted variation both in number of lambs born and in lamb survival, exemplified in Table I for three hill breeds. The dimension added by a high fertility breed like the Finnish Landrace is obvious. Cross-breeding is indicated not only to take advantage of the breed differences but because cross-bred ewes may well show hybrid vigour both in terms of number of lambs born and surviving. Table II shows a comparison of five cross-bred types of ewe produced by mating Blackface females to sires of the breeds shown. The cross-bred ewes in turn were all mated to rams of one breed. The Finnish Landrace sires increased the number of lambs weaned per ewe mated by about half a lamb above the flock average, and the Merino decreased it by about the same amount. The litter weights produced, though closely correlated with lamb numbers, show a narrower range of merit.

TABLE II
LAMB PRODUCTION OF CROSSBRED EWES*

Sire of ewe	Lambs weaned/ewe mated		Total †litter weight at weaning (kg.)
	1st year	Av. of 2nd & 3rd	
Border Leicester	0·78	1·40	127
Clun Forest	0·71	1·35	117
Dorset Horn	0·70	1·37	122
Finnish Landrace	0·82	1·91	139
Merino	0·38	0·99	89

*(from Donald, Read and Russell, 1968
†Total for three lamb crops, years 1-3

As an example of what might be expected from using Finnish Landrace sheep on a wider scale, Purser (1969) calculated, by extrapolation from the first available experimental results, that to use rams with $\frac{3}{4}$ Border Leicester and $\frac{1}{4}$ Finn blood in place of pure Border Leicester (where these are at present used) would yield an extra six-and-a-half thousand tons of lamb carcases—and this in spite of a somewhat slower growth rate attributable to the Finn compared with the Border Leicester. Clearly, this is only one of several situations where the introduction of new breeds has a place in British sheep production.

Maternal Effects

Breeds and individuals within breeds, because they differ in size, in the uterine environment they provide and in their milk production, can markedly affect the size and growth of their lambs. Cross-breeding, in particular, can be useful in manipulating the variables.

Body Size and Growth Rate

Breed differences in body size are appreciable in magnitude. Most of the differences in growth rate are a function of differences in mature body size. Little hybrid vigour can be expected from cross-breeding. Mature body size is fairly strongly inherited and selection for it should be effective, but lamb weight at weaning and growth early in life is subject to marked maternal effects and hence less easy to change by selection within breeds. In spite of somewhat higher estimates for the heritability of growth rate or carcase weight than for fertility, selection on the former traits would yield less extra meat for the nation (one thousand tons per year according to Purser, 1969) than would attention to fertility, because the selection intensity would be lower.

Carcase Attributes

These do not lend themselves to easy generalisations. Carcase quality, in particular, seems to be as much the subject of opinion as of fact. The feeding, management, and the age and weight of the animal at slaughter are all more important than genetic variation in other aspects of "quality." Although breeds differ in conformation, differences in the meat yield appear to be very much smaller—a point which farmers might do well to stress in their dealings with the meat trade.

Efficiency of Food Utilisation

This characteristic may well become of importance in intensive lamb production. As yet there is extremely little information in respect of differences between or within breeds of sheep. Blaxter, Clapperton and Wainman (1966), in one of the few relevant experiments, concluded that when intake was related to true maintenance requirement, breed differences were not significant. Experience in other species, however, would make it surprising if genetic variation

in efficiency were not discovered to play some part in the very considerable individual variation in intake and growth rate known to exist. The economic rewards for even small improvements could be considerable.

Wool

The uncertainty in the future market for wool suggests that it would be inadvisable to put effort into changing wool at the expense of any of the other attributes. From the geneticist's point of view the fleece and its components are pliable material. There are great differences among breeds which have been well documented and in commercial terms well categorised. Hybrid vigour is not an important expectation for wool attributes. Breed substitution and cross-breeding are, however, easy ways of changing the average type and selection, as exemplified in the Australian Merino, is an effective means of change (see, for example, Turner, 1956).

Disease and Mortality

No veterinarian needs reminding of the high cost to the livestock industry, including sheep farmers, of losses by death, disease and ill thrift. For convenience three broad categories of disease can be considered.

(a) " Hereditary defects " such as skeletal malformations, cud spilling or congenital photosensitivity.
(b) Diseases involving pathogens.
(c) Metabolic disorders.

Young (1967) has reviewed the literature on hereditary diseases in livestock in general and has discussed modes of inheritance and methods of control. Even in the category of disease where the mode of inheritance has been found to be simple and only one or two genes are involved, it is not uncommon for environmental variation and the genetic background in which the deleterious genes occur to modify the expression. As Young points out in his article, simply to divide diseases into genetic and non-genetic is inaccurate. In this category of disease, however, the feasibility of a genetic solution is not in doubt and only the strategy and costs require careful consideration.

Diseases involving pathogens present a more complex problem. The case for purely veterinary treatment, even when available, is not as clear as might have been thought some years ago. The restrictions placed on the use of antibiotics as feed additives, and the greater caution now exercised in their use both in veterinary and human medicine, illustrate the point born of evidence of the phenomenon of infectious drug resistance and the acknowledged ability of pathogens to evolve resistant forms. In addition, there is a theoretical possibility, stressed in eugenics, that treatment may preserve genetically inferior stock for breeding. The practical importance of this would be difficult to establish and it is clearly not an experiment that many commercial farmers would or should be willing to undertake. It would also be easy to overstate the case for genetic control since the degree of involvement of the hereditary constitution of the host (not to mention the heredity of the pathogen) is generally unknown. Dickinson and Mackay (1967) and Dickinson (1969) have set forth the arguments and evidence in a way which will repay reading. As stressed by these authors, resistance and susceptibility conceived in genetic terms are relative, and to breed for resistance without a fuller definition of what is implied need not even be desirable lest it lead, for example, to clinically unaffected individuals which act as carriers and invite clinical disease in changed circumstances. Genetic investigation, often at a fundamental biological level, will undoubtedly help to solve a number of otherwise intractable problems such, for example, as scrapie, but there is enough evidence already to make easy generalisations from one disease to another untenable.

Metabolic disorders which involve deficiency, excess or imbalance of nutrients are clearly rectifiable by nutrition or management except in those few cases where the demand for nutrient temporarily outstrips all capacity of the animal to ingest enough. Recent work, reviewed by Wiener and Field (1971), has shown, however, that breeds vary in their susceptibility to disorders such as swayback, copper poisoning, or hypomagnesaemia, when under apparently similar conditions, and that some of the well-recognised individual variation in the clinical manifestation of metabolic troubles has a hereditary component. This suggests two potential uses of genetic investigation in this area: the first, most likely to be useful for highly intensive husbandry systems, is to investigate the nature of genetic differences in the response to the particular nutritional and environmental stresses being met, and then to modify the management to suit the inherited needs of the animals. The second, for extensive conditions where it would be too costly to modify the environment, to produce specially adapted strains. It is very unlikely that either could be done by attention only to the clinical manifestation of disorder. Progress is much more foreseeable in terms of understanding the biochemistry involved and the interactions which lead alternately to normal function or to disorder.

" Hardiness " assumes the ability to withstand stresses of undefined kinds arising from malnutrition, cold and disease, and from interactions of these. Future progress must come from attending to the components of " hardiness." As pointed out by Slee (1967), cold resistance is now a recognisable physiological character and can be added to the list of those showing genetic variation; but effective methods of selection, either between or within breeds, are as yet unclear.

In the meantime the farmer is left with a choice among breeds some of which appear on reputation or on limited experimental evidence to be more resilient than others in some circumstances. And he is left with the better-established fact that in terms of lamb survival, and possibly in other aspects of thrift and fitness, cross-bred animals have a distinct advantage. In a later stage of the ABRO sheep experiment referred to in Table I, cross-bred

lambs out of cross-bred mothers involving the Blackface, Cheviot and Welsh breeds had on average only two-thirds of the mortality of the three pure breeds. The poorest of the three breeds had four times the losses of the best of the cross-breds which, in turn, was slightly better than the best of the pure breeds; in-breds also fared worse than did non-inbreds. Extrapolated to a national scale, where three to four million lambs die annually, replacement of half the present pure-bred ewes with crosses, might well provide an extra seven to 10 thousand tons of meat each year from the extra lambs saved. The precise biological reasons why this cross-bred advantage occurs, or the in-bred disadvantage, may indeed be basic to an understanding of genetic disease resistance. Merely to attribute the difference to the greater heterozygosity of the one compared with the other is to beg the question.

Conclusions

Attention in this article to the scope of increasing productivity through breeding has been at the expense of discussing the operational details and their attendant costs. These will often determine whether a theoretically desirable goal is worth pursuing in practice. Also, no more than mention can be given to the likelihood that genetic change in one production trait, itself usually a complex of several components, will be accompanied by changes in other traits. For example, increasing the mature size of ewes in pursuit of larger lambs would lead to greater food requirements although it might also lead to a small increase in fertility. Hence the advice of many geneticists to obtain size in lambs through the ram and to use the smallest ewe to produce the lambs consistent with other requirements.

It also needs to be said that while genetic improvement will permanently change the potential production of the sheep, management must be able to take advantage of the change. Even the increased survival of cross-bred lambs from cross-bred mothers, the nearest to a free bonus, makes some extra demands on feed.

This article has said nothing about those pedigree breeders who are still capable of making money from the outward appearance of sheep. Their success in manipulating genes which are but little modified by environment is unfortunately little guide to the requirements for improving commercially viable traits which are under less close genetic control. Thus geneticists tend, particularly in relation to selection, to think in terms of large or national schemes such as those being organised by the Meat and Livestock Commission where the individual breeder is a co-operator and beneficiary but not a sole agent. With the present stratified and hierarchical structure of the British sheep industry, genetic changes in the right place and of the right type can have far-reaching results for most commercial producers apart from the immediate advantage which can be gained by them from further cross-breeding or changes of breeds. The two traits most likely to repay genetic improvement are prolificacy of ewe and growth rate of lamb. Reduction in lamb mortality expected to result from additional cross-breeding, while arising as a bonus to other action, might also be added as an aim.

The sheep farmer in Great Britain is fortunate in that, with the exception of controls on the import of new breeds, he has virtually no administrative hindrance to the process of genetic improvement possible, using the vast reservoir of genetic variability of the world's sheep breeds and the individual variation within them. He has the choice of increasing production or of maintaining production with smaller numbers; in either event attention to breeding will improve efficiency.

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BREED VARIATION IN LAMBING PERFORMANCE AND LAMB MORTALITY IN COMMERCIAL SHEEP FLOCKS

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SUMMARY

Two surveys were conducted on commercial farms in England, Wales and Scotland to ascertain whether breeding contributed to variation in the number of lambs born per ewe, in lamb mortality and in the number of lambs remaining to be weaned per ewe. Each flock comprised two or more breed groups, but within flocks differences in breed were often quite small.

In one survey of 74 flocks (average size 198 ewes, comprising 175 breed groups) the lambing percentage averaged around 150% and the lamb deaths to weaning (including stillbirths) around 9%. Within flocks there were statistically significant differences in the number of lambs born and weaned per ewe attributable to the breed of lamb and of its dam and sire. Crossbreeding was associated with a higher weaning percentage. Lamb mortality differed significantly among breeds and crosses of lamb. Lambing performance varied with type of farm.

The second survey was a comparison of different crossbred types of dam, themselves the offspring of three breeds of sire and seven of ewe. Thirty flocks participated, providing 29 sets of records for 1-year-old females producing on average 120% lambs and losing through death (including stillbirths) 25% of lambs born, and 10 sets at 2 years old, with 176 lambs per 100 ewes lambing and 11% of the lambs born dying before 8 weeks old. Variation attributable to the crossbred type of the dam and to the breed of the dam's sire was significant for lambing and weaning percentage and the incidence of lamb mortality.

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INTRODUCTION

EVIDENCE on the incidence of lamb mortality, derived mostly from institutional and experimental flocks, suggests that in the United Kingdom between 10 and 25% of lambs born commonly die. A recent survey by the Meat and Livestock Commission (1972) estimates pre-weaning losses in recorded flocks of crossbred ewes at about 13% of lambs born. Neither institutional nor recorded flocks may be typical of commercial flocks in general, extrapolation from these figures is therefore difficult. However, the figures suggest that from 1½ to 4 million lambs die annually in Great Britain.

Evidence from experimental flocks also suggest that breeds may differ in the incidence of lamb mortality and that crossbreeding may be advantageous.

It was decided therefore to conduct a survey to see whether under commercial farm conditions the number of lambs weaned per ewe could be attributed to differences among breeds or breeding systems. The two components of the weaning percentage which were considered separately were the number of lambs born per ewe and the incidence of lamb mortality, from whatever cause, between birth and weaning. The results are reported in this paper.

MATERIAL AND METHODS

This paper deals with two separate surveys. The first, which will be referred to as the 'general' survey, involved collaboration between the Animal Breeding Research Organisation, Livestock Husbandry Officers of the National Agricultural Advisory Service (as it then was) in England and Wales and Advisory Officers attached to the three agricultural colleges in Scotland (both groups of officers will be referred to hereafter as advisory officers). In the course of this survey there was also close collaboration with members of the Veterinary Investigation Service of these three institutions. Most of the data were collected by advisory officers but a proportion by veterinary officers. Subsequently, data of a second survey were made available from commercial flocks chosen for purposes of breed testing by a breeding company, Thornbers (Agriculture) Ltd.

General survey

This was carried out on a pilot scale in 1967 and on a larger scale in 1968. Data from both years were used. Two flocks common to both years were included twice in the analysis. Restrictions imposed by an outbreak of foot and mouth disease in 1967–68 closed a large area of the country to the survey and curtailed movement in others, thus preventing the survey from reaching the intended number of flocks.

Flocks were chosen by the advisory officers. The prerequisites were that each flock should comprise two or more groups of identifiably different breeds or crosses kept together except at mating, that the ewes of the different groups should be of equivalent age, and that the farmers concerned were willing to provide unselected information. There were on average 2·4 breed groups (range 2–6) in each of the flocks included in the final analysis. Average flock size was 198 females at lambing. The total sheep population surveyed thus comprised almost 15 000 breeding females. Thirty-eight of the

flocks were situated in England and Wales and 36 in Scotland. All flocks included in the analysis were chosen prior to the onset of lambing. Each of the flocks provided information on the number of lambs born and the numbers dead (including stillbirths) before weaning. Additional information was sought on mortality of single-born and twin-born lambs, on the type of rearing and management of the flock, on the age structure of the flock and on the type of farm, e.g. hill farm, low land, arable farm, etc. This additional information was not provided for all flocks and analyses involving these additional factors were therefore based on smaller numbers of flocks or excluded if a large proportion were unclassified.

Thornber survey

The flocks included were chosen by field officers of Messrs Thornbers (Agriculture) Ltd for a comparison of different crossbred types of ewe. These were the progeny of three breeds of ram, Border Leicester, Colbred and Teeswater, mated to seven breeds of female—six of them hill breeds and the Clun Forest. Information was recorded in 1963 and 1964 on the number of ewes mated and lambing and on the number of lambs born and dying (including stillbirths) before 8 weeks of age. This was the only information used for the present analysis although the breed comparisons were designed to serve wider objectives. Thirty-nine sets of information (flocks within year) were available in the survey, involving 30 flocks—nine of them twice (in successive years). In 29 of the flocks all the females were 1-year-old at lambing and only in the nine flocks included twice and one additional flock were 2-year-old females used. There were on average 5 breed groups per flock (range 2–15) and the average flock size at lambing was 100 females and the total number of breeding females in the survey about 4000. The farms involved covered a wide area of the country and included both arable and grassland. The management system was not prescribed for the flocks of the selected farms but they were considered to be well managed. The sheep were sold by Thornbers to the co-operating farmers who undertook to provide records. These were kept by the farmers themselves under the supervision of field officers employed by Thornbers. Thornbers also provided the rams which were mated to the females and, although within any one flock the same breed of ram was used, the use of different breeds of ram in different flocks allowed limited comparisons among sire breeds.

Statistical methods

The surveys were designed so that the effects of breed and other within-flock factors could be examined with the effects of between-flock factors eliminated. The main statistical analyses required the fitting of a model which included terms for flocks and for the within-flock factor under consideration. Because of the number of flocks involved the direct approach of fitting constants to the full model was not feasible. Instead a method outlined by Patterson (1971) was adopted in which the measure of performance and the within-flock terms were adjusted for differences between flocks before estimating the effects of the within-flock factor free of flock differences.

The following measures were computed for each group:

(*a*) number of lambs born (including stillbirths) as a percentage of the total number of females lambing,
(*b*) number of lambs weaned (the difference between numbers born and numbers that died) as a percentage of the total number of females lambing,
(*c*) number of lambs which died (including stillbirths) as a percentage of the total number of lambs born.

As mortality rates lay mostly in the range from 0 to 25% of the numbers born, the proportions could reasonably be expected to be binomially distributed; a transformation was therefore considered necessary. The logit transformation was tried but gave greater weight to lower percentages and tended to produce results which were not completely consistent with differences between the percentage of lambs born and the percentage of lambs weaned. The arcsine transformation proved to be more satisfactory in this respect and was applied to measure (*c*).

The two surveys were analysed separately. The various models were fitted, using a weighted least squares technique. Measures (*a*) and (*b*) were weighted in proportion to the total number of females lambing. Measure (*c*) was weighted in proportion to the total number of lambs born. The values presented in the Tables are therefore weighted means. Means for measure (*c*) were computed on both the radian and percentage scales and both are given in the Tables, since standard errors can be appropriately applied only to differences in the radian scale. The probabilities presented for measure (*c*) in Tables 3 and 9 have been deduced from analyses on the radian scale.

For some of the analyses the fitting of the model, which adjusted for flocks, required the omission of a small number of breeds. This occurred when a breed appeared in a flock alongside another breed in such a way that it could not be linked to further breeds in other flocks.

The results for the nine flocks of the Thornber survey and the two in the general survey which were recorded in two successive years, were treated as independent sets of observations in the analyses.

In Tables where standard errors of differences are given the maximum value applies broadly to comparisons involving small numbers of groups and the minimum values to those involving large numbers of groups.

RESULTS

The principal breeds and crosses among the 62 represented in the two surveys are shown in Table 1.

General survey

Table 2 presents the general survey data classified in a number of different ways without adjustment for between-flock differences. The averages indicate the actual levels of performance in the population sampled and provide a base line from which changes might be sought. The possibility of confounding influences must be recognised in the averages shown in Table 2, for example between types of farm and breed, although at least two breed types co-existed in each flock.

TABLE 1

Frequency of the parental breeds and crosses involved in the surveys

		Number of groups			
		General survey		Thornber survey	
Breeds		Sire	Dam	Sire	Dam
Border Leicester		16	3	—	—
Cheviot (NC)		7	15	—	—
Cheviot (SC)		5	4	—	—
Clun Forest		11	23	—	—
Colbred		7	—	—	—
Dalesbred		2	4	—	—
Dorset Down		18	1	15	—
Dorset Horn		3	2	—	—
Exmoor		1	4	—	—
Hampshire Down		9	—	12	—
Hexham Leicester		3	—	—	—
Scottish Blackface		14	28	—	—
Suffolk		52	1	136	—
Swaledale		3	10	—	—
Teeswater		3	—	—	—
Welsh Mountain		—	2	—	—
Other breeds (5)†		3	2	—	—
Crosses					
Border Leicester	× Cheviot (type unspecified)	—	21	—	8
	× Clun Forest	—	1	—	6
	× Rough Fell	—	—	—	2
	× Scottish Blackface	—	8	—	19
	× Swaledale	—	—	—	6
	× Welsh Mountain	—	2	—	4
	× Other breeds (1)†	—	1	—	—
Clun Forest	× (Suffolk × Clun)	—	4	—	—
Colbred	× Cheviot (NC)	—	2	—	19
	× Cheviot (SC)	—	1	—	14
	× Clun Forest	—	3	—	28
	× Rough Fell	—	—	—	2
	× Scottish Blackface	—	2	—	26
	× Swaledale	—	1	—	22
	× Welsh Mountain	—	—	—	11
	× Other breeds (1)†	1	—	—	—
Dorset Down	× Suffolk	—	—	12	—
	× Other breeds (2)†	—	2	—	—
Finnish Landrace	× Dorset Horn	10	—	—	—
	× Other breeds (3)†	3	—	—	—
Southdown	× Dorset Down	—	—	5	—
	× Hampshire Down	—	—	4	—
Suffolk	× Border Leicester	3	1	—	—
	× (Border Leicester × Cheviot)	—	13	—	—
	× Hampshire Down	—	—	9	—
	× Other breeds (4)†	1	4	—	—
Teeswater	× Cheviot (NC)	—	—	—	6
	× Clun Forest	—	—	—	6
	× Rough Fell	—	—	—	2
	× Swaledale	—	4	—	8
	× Welsh Mountain	—	—	—	4
Other crosses (4)†		—	6	—	—
Total number of groups		175	175	193	193

† Number of different breeds and crosses.

TABLE 2

General survey: the unadjusted average performance of groups of sheep classified in different ways

Classification factors	Number of groups	Number of lambs		
		Born†	Weaned†	Dying‡
Type of farm				
Hill	41	132	121	8·1
Upland	16	165	149	9·7
Livestock	4	164	152	7·4
Grassland	24	159	147	7·9
Mixed	46	156	141	9·5
Lowland	14	159	140	11·8
Arable	30	178	159	10·7
Breeding system				
Purebred dam, purebred lamb	36	137	124	9·2
Purebred dam, crossbred lamb	63	149	137	8·2
Crossbred dam, crossbred lamb	76	166	149	10·1
Selected breeds of dam of the lamb				
Scottish Blackface	28	139	127	8·9
NC Cheviot	15	161	143	11·4
Swaledale	10	117	111	4·8
Clun Forest	23	163	150	8·0
Border Leicester × Blackface (Greyface)	8	171	151	12·0
Border Leicester × Cheviot§ (Half bred)	21	180	162	10·0
Suffolk × Half bred	13	170	154	9·5
Selected breeds of sire of the lamb				
Scottish Blackface	14	130	119	8·7
NC Cheviot	7	136	121	11·1
SC Cheviot	5	127	105	17·1
Clun Forest	11	164	151	7·6
Border Leicester	16	149	136	8·8
Dorset Down	18	177	159	10·0
Hampshire Down	9	172	159	7·7
Suffolk	51	163	147	10·0
Colbred	7	155	121	9·4
Finnish Landrace × Dorset Horn	10	154	140	9·4
Size of flock				
100 or less	34	160	144	9·6
101–200	68	159	144	9·4
201–300	42	157	139	11·3
301–400	15	147	134	8·9
401 or over	16	148	138	7·1
Age of dam				
1-year-old	6	125	97	22·3
1st parity (2-year-old)	9	160	140	12·3
2nd and 3rd parity	30	157	143	8·8
4th parity	21	164	150	8·4

† Number of lambs per 100 ewes lambing.
‡ Number of lambs per 100 lambs born.
§ Type of Cheviot (North or South Country) not specified.

The classification by type of farm did not lend itself to adjustment for between-flock differences. Attention is drawn to the differences observed among the farm types in the unadjusted data (Table 2). Hill farms were associated with the lowest and arable farms with the highest lambing and

weaning percentages. The classification of the farms by type was made by the advisory officers visiting them. Since no strict criteria were laid down for these definitions, some overlap must be expected.

As also seen in Table 2, breeds traditionally associated with hill farms had lower lambing and weaning percentages, but not necessarily higher mortality rates among lambs, than breeds normally associated with less harsh farm conditions.

The further statistical analyses were aimed at providing values which would indicate the contribution of the separate effects of the several classification factors to the variation observed in the performance of the groups of sheep.

Breed effects. These have been classified in four different ways:

(1) by the breeding system, grouping the dams and their offspring as purebred, or crossbred,
(2) by breed of dam,
(3) by breed of sire, and
(4) by breed of lamb.

As seen in Table 3, most of these factors when taken in turn represented significant sources of variation for the percentage of lambs born and weaned

TABLE 3

General survey: the probability that variation attributed to the factors shown could be due to chance alone (adjusted for flock differences)

Factor	Lambs born†	Lambs weaned†	Lambs dying‡
Breeding system	0·12	0·04	>0·20
Breed of dam	<0·01	<0·01	>0·20
Breed of sire	0·07	0·03	>0·20
Breed of lamb	0·02	0·04	0·05
Flock size	(>0·20	>0·20	0·01)§
Age of dam	>0·20	>0·20	0·18

† Number of lambs per 100 ewes lambing.
‡ Number of lambs per 100 lambs born (transformed to radian scale).
§ Adjusted for farm type only.

to ewes lambing, but only marginally so for lamb mortality (lambs dying per 100 lambs born).

Tables 4, 5 and 6 give the lambing and weaning percentages and the percentage lamb mortality for the breeding system and for the dam and sire breeds which were represented by at least seven groups in the survey.

The results in Table 4 suggest that, on a within-flock basis, there appeared to be an increase in the number of lambs born and weaned per 100 ewes lambing associated with crossbreeding of the lamb but not of the dam. The unadjusted averages in Table 2 had suggested a further beneficial effect on performance of using crossbred dams. The differences between the two sets of results may suggest that the farms where crossbreeding took place provided a more favourable environment. However, the difference may also reflect a smaller 'difference' in terms of breed composition of the groups of dams being compared within flocks than when the survey as a whole is considered; this point will be discussed later. The breeds involved in the

TABLE 4

General survey: breeding system (adjusted for flock differences)

Breed of		Number of groups	Number of lambs		
Dam	Lamb		Born†	Weaned†	Dying‡
Pure	Pure	36	152	135	10·7 (0·318)
Pure	Cross	63	159	144	9·1 (0·295)
Cross	Cross	76	160	144	10·0 (0·304)
SE of difference—max.			5·9	5·8	−(0·029)
SE of difference—min.			3·5	3·5	−(0·018)

† Number of lambs per 100 ewes lambing.
‡ Number of lambs per 100 lambs born; figures in parentheses are as calculated on radian scale.

crosses are not necessarily the same, or in the same proportions, as in the purebred groups. The results cannot therefore be interpreted as evidence for heterosis.

Table 5 shows results for the selected breeds of dam. For the number of lambs born and weaned per 100 ewes the effect of adjustment for between-flock differences has been to reduce variation quite markedly for these particular breeds compared with the unadjusted levels. As would be expected, the difference between the hill breeds and other breeds and crosses is much

TABLE 5

General survey: selected breeds of dam of the lamb (adjusted for flock differences)

Breed of dam	Number of groups	Number of lambs†		
		Born	Weaned	Dying
Blackface	28	163	155	5·0 (0·227)
NC Cheviot	15	162	149	8·5 (0·293)
Swaledale	10	132	129	0·6 (0·172)
Clun Forest	23	166	142	14·9 (0·356)
Border L × Blackface (Greyface)	8	142	128	11·6 (0·330)
Border L × Cheviot (Half bred)	21	164	141	14·8 (0·386)
Suffolk × Half bred	13	163	137	16·5 (0·419)
SE of difference—max.		21·3	20·9	−(0·129)
SE of difference—min.		6·2	6·1	−(0·034)

† See Table 4.

reduced. When compared on a (statistically) common farm environment the three hill breeds had a lower death rate among their lambs than the other breeds with a consequent advantage to the number of lambs weaned by the hill breeds. In respect of lamb mortality, the statistical adjustment has left the relative ranking of the three hill breeds (seen in the raw averages of Table 2) unchanged, but has highlighted the low mortality among lambs born to Swaledale ewes.

Table 6 shows differences among selected breeds of sire. Adjustment for flock differences again had the effect of increasing the apparent productivity attributable to the three hill breeds relative to the other breeds. The

South Country (SC) Cheviot was included mainly for comparison with the North Country (NC) Cheviot although the number of groups involved was less than the arbitrary seven. Although for all sire breeds the variation in lamb mortality was not significant, the high mortality among the Cheviot, particularly the South Country type, suggests a real effect.

Although some confounding of sire and dam breeds might be expected in practice, there was little evidence of it in the present survey. In approximately 70% of the flocks the different groups within a flock had either the same breed of dam or the same breed of sire. In the other 30% of flocks, a particular association of sire and dam breeds within one flock did not necessarily occur in other flocks. Thus, the results in Tables 5 and 6 could be expected to represent real effects of the parent breeds.

TABLE 6

General survey: selected breeds of sire of the lamb (adjusted for flock difference)

Breed of sire	Number of groups	Number of lambs† Born	Weaned	Dying
Blackface (Scottish)	14	141	126	10·6 (0·322)
NC Cheviot	7	152	127	15·6 (0·392)
SC Cheviot	5	138	107	20·6 (0·470)
Clun Forest	11	174	159	8·8 (0·276)
Border Leicester	16	151	136	10·6 (0·329)
Dorset Down	18	172	157	8·4 (0·282)
Hampshire Down	9	170	152	10·6 (0·314)
Suffolk	51	164	149	8·7 (0·281)
Colbred	7	173	156	10·6 (0·325)
Finnish Landrace × Dorset Horn	10	166	156	6·0 (0·239)
SE of difference—max.		14·4	14·0	−(0·072)
SE of difference—min.		5·6	5·4	−(0·028)

† See Table 4.

Lamb's breed. Although as seen in Table 3 variation attributable to the breed or cross of lamb was statistically significant, too many types were involved, many of them occurring only once, for a sensible separate consideration.

Flock size. The number of ewes at lambing was not significantly associated with lambing or weaning percentage. A trend seen in the unadjusted values of Table 2 disappeared after adjustment for farm type (Table 7). The variation in lamb mortality, however, was significant ($P < 0{\cdot}05$). It appears that the lowest mortality was among lambs in the largest flocks. Unfortunately no information is available from the survey on whether this result reflects the kind of management and labour used to look after the sheep in different sizes of flock.

Age of dam. The nature of the data did not allow the inclusion of the youngest age group when adjustment for flock differences was also made. The figures (Table 8) after this adjustment show that females lambing for the first time at 2 years old had lower lambing and weaning percentages than ewes of later parities. Whilst the variation among the age classes in general was not significant (with one exception) this included a class of 98 groups

specified as being of 'regular or mixed ages' and another class of 11 groups where age was not specified at all. Table 8 excludes the results for these indeterminate classes. The figures before adjustment (Table 2) also indicate that, as expected, females lambing for the first time at approximately 1 year old had a lower lambing percentage and a higher mortality among lambs born and a correspondingly much lower weaning percentage than did either females which lambed for the first time at 2 years old or females of later parities.

TABLE 7

General survey: size of flock (adjusted for farm type only)

Number of ewes at lambing	Number of groups	Number of lambs†		
		Born	Weaned	Dying
100 or less	34	159	144	9·1 (0·292)
101–200	68	161	146	9·2 (0·295)
201–300	42	160	143	10·9 (0·323)
301–400	15	157	142	9·7 (0·307)
401 or over	16	152	142	6·5 (0·252)
SE of difference—max.		9·4	8·9	−(0·032)
SE of difference—min.		5·5	5·2	−(0·018)

† See Table 4.

TABLE 8

General survey: age of dam (adjusted for flock differences)

Age or parity of dam	Number of groups	Number of lambs†		
		Born	Weaned	Dying
1 year old	6	—	—	—
1st parity (2 years old)	9	139	124	10·6 (0·318)
2nd and 3rd parity	30	167	145	12·9 (0·349)
4th parity	21	161	147	8·6 (0·282)
SE of difference—max.		21·5	21·8	−(0·103)
SE of difference—min.		9·2	9·3	−(0·030)

† See Table 4.

Thornber survey

The results involving breed comparisons are given in terms of comparisons within flocks and ages of dam. Apart from variation attributable to breeds the only other factor separately recorded was age of dam. It should be noted that in the majority of flocks the females were lambing for the first time at 1 year of age and only a relatively small number of flocks had 2-year-old females.

Table 9 shows the probability that variation attributable to the breed factors could be due to chance. The effect of breed of dam was highly significant but the contributions of the breeds of the lamb's maternal grandmother (dam's dam) and grandfather (dam's sire) varied in significance. Since within any flock only one breed of ram was used as the father of the

lambs the effect of breed of sire could not be analysed within flock but adjustment was made for age of dam (i.e. the mate of the ram).

Breed of dam. Eighteen of the 21 possible crosses of dam, generated by their three breeds of father and seven of mother, were represented in the survey. The number of lambs born per 100 females lambing varied from 111 to 139, the numbers weaned from 57 to 111 and the mortality of lambs born from 14 to 52%. One of the crossbred types fell outside these ranges. It was represented by only a very small number of females (though spread across four flocks) which were unfortunate to lose most of the few lambs born. There was a statistically significant interaction between breed of dam's dam and that of the dam's sire in respect of the number of lambs born and weaned, but not for lamb mortality. This arose mainly from the better performance of the Colbred males (compared with Teeswater and Border Leicester) when crossed with the North Country Cheviot and Welsh Mountain

TABLE 9

Thornber survey: the probability that variation attributed to the factors shown could be due to chance alone (adjusted for flock differences and age of dam)

Factor	Lambs born†	Lambs weaned†	Lambs dying§
Crossbreed of dam	<0·01	<0·01	<0·01
Breed of dam's dam	<0·01	0·11	0·16
Breed of dam's sire	0·04	<0·01	0·04
Breed of sire	(<0·01	<0·01	0·03)§

† Number of lambs per 100 ewes lambing.
‡ Number of lambs per 100 lambs born (transformed to radian scale).
§ Adjusted for age of dam only.

females. The results are, however, more easily presented in terms of the breeds of the parents of the ewes.

Breed of maternal grandparents of the lambs. The results are shown in Table 10. Variation attributable to the maternal grand-dam of the lambs is seen in the range from 120 to 137 in the number of lambs born per 100 ewes lambing whilst weaning percentage ranged from 94 to 111. Mortality rates varied from 20 to 26%. Among the three breeds of maternal grandsire of the lamb the Colbred was associated with marginally the highest lambing percentage and the lowest mortality among the lambs born. In consequence this breed came out best in terms of the number of lambs weaned per 100 ewes lambing.

Breed of sire. In 30 cases (flocks within year) Suffolk rams were used as fathers of the lambs. Three other breeds or crosses of ram were used in two flocks each and a further three breeds in one flock each. The values calculated for 'breed of sire' will not therefore be separately presented because the substantial confounding with flock differences may make them misleading. Without adjustment, or after adjustment only for the age of mate, the variation attributable to the breed of sire appeared to be a significant source of variation for lambing and weaning percentage and for lamb mortality (Table 9).

Age of dam. Since within any flock in any one year only one age class of female was used, the result shown in Table 11 could not be adjusted for flock

differences. Also, only one of the flocks with 2-year-old females contributed information in the first year of this survey and no 1-year-old females were present in the second year. The results must therefore be accepted with caution, but they follow expectation in that females lambing for the first time at 1 year old produced fewer lambs and had a higher mortality rate among these lambs than females which lambed, mostly for the second time, at 2 years old.

TABLE 10

Thornber survey: breed of dam's parents (adjusted for flock differences and age of dam)

	Number of groups	Number of lambs†		
		Born	Weaned	Dying
Breed of dam's dam				
Blackface (Scottish)	45	136	109	20·1 (0·438)
NC Cheviot	33	132	102	24·1 (0·488)
SC Cheviot	14	120	94	22·9 (0·453)
Swaledale	36	135	111	19·8 (0·423)
Welsh Mountain	19	123	96	22·2 (0·473)
Rough Fell	6	132	103	23·8 (0·505)
Clun Forest	40	137	103	26·1 (0·518)
SE of difference—max.		9·0	13·4	−(0·104)
SE of difference—min.		2·9	4·4	−(0·034)
Breed of dam's sire				
Border Leicester	45	131	98	25·6 (0·517)
Colbred	122	135	107	22·2 (0·459)
Teeswater	26	126	92	27·1 (0·545)
SE of difference—max.		4·2	6·0	−(0·047)
SE of difference—min.		3·2	4·5	−(0·036)

† See Table 4.

TABLE 11

Thornber survey: unadjusted average values classified by age of dam

Age of dam	Number of groups	Number of lambs†		
		Born	Weaned	Dying
1 year old	147	121	88	26·9 (0·525)
2 years old	46	177	155	12·7 (0·333)
SE of difference		2·5	4·1	−(0·029)

† See Table 4.

DISCUSSION

The average level of mortality among lambs in the general survey, averaging around 9 to 10%, was unexceptional but less than reportedly occurs in some years. The range of lamb mortality in the separate flocks varied from 1 to 21%. The higher mortality rates of lambs in the Thornber survey, can, apart from the fact that the observations pertain to different years, be attributed to the use mostly of females lambing for the first time at 1 year old.

As seen from the results given earlier, the mortality among lambs born to the 2-year-old females was of the same order in both surveys.

It is not known whether the levels of performance achieved in these flocks is typical of other flocks. Willingness to cooperate with advisory and veterinary officers to provide the necessary information might suggest that the levels of management were above average. The average level of lambing performance of crossbred ewes in the general survey appears to be slightly higher than that summarized for the performance of commercial crossbred ewes in 99 flocks recorded by the Meat and Livestock Commission (1972) over the period 1970 to 1972. By the same token, such recorded flocks may also be 'above average'. In the MLC recorded flocks, the average number of lambs born per 100 ewes lambed was 153, the numbers weaned 134, and the number of lambs dying was 12·5 per 100 lambs born compared with the figures of 166, 149 and 10·1 respectively from the corresponding category of sheep (Table 2) in the present study.

The main purpose of the present surveys was to ascertain whether, under commercial farm conditions, breed variation contributed to lamb numbers born, to lamb mortality and to the resultant numbers weaned.

The relationship between lambing percentage and lamb mortality among breed groups within flocks was low ($r = 0{\cdot}06$ for the general survey and $r = 0{\cdot}04$ for the Thornber survey). But on the basis of the data for the separate breeds shown in Tables 5, 6 and 10, the relationship seems more complicated than implied by a low overall correlation. The data in these Tables suggest that increasing the lambing percentage through the dam's breed may involve increasing lamb mortality, but that the paternal contribution could have the opposite effect. Data from the present surveys do not provide an adequate basis for testing these possibilities further.

Comparison of the unadjusted results with those after adjustment for between-flock differences shows that breed, breeding system and 'farm environment' were partly confounded and that conclusions about the relative merit of breeds are more reasonably deduced from the adjusted values, although the possibility of breed × environment interactions, which could not be estimated, might add further complexities to decisions about choice of breed or breeding systems.

It should be noted that the extent of the differences in breed composition encountered between the groups within the majority of the flocks was quite small. In the case of the general survey, 50% of the flocks maintained only one breed or crossbred type of female and the breed variation tested was that attributable to different sire breeds mated to these ewes. In a number of flocks the sires themselves were crossbred, differing from each other only partially in breed composition. For the other 50% of the flocks in the general survey where there was some maternal breed variation it only rarely constituted a difference between two distinct breeds. In many such flocks only one breed of sire was used. In the Thornber survey, all the dams were crossbred, and whilst the design of the trial allowed for many more comparisons within flocks than in the general survey, many of these comparisons involved a breed difference in respect of only one of the parents of the dam. Within any one flock in the Thornber survey, all females were mated to the same breed of ram; the lambs thus differed in their breeding by only half the amount of their mothers. In other words, the variation attributable to breeding examined in these surveys represents only a proportion—in the

case of the lambs perhaps between one-half and one-quarter—of that possible for the breeds involved. In these circumstances the fairly clear suggestion that breed and breeding system significantly affected lambing and weaning percentage is the more noteworthy. In respect of the number of lambs dying the evidence is more equivocal. The results from the general survey suggested that within flocks the differences among 'breed types' of lamb were significant but not those attributable to breeding system, to the breed of dam, or to the breed of sire. The evidence from the Thornber data suggested that there were significant differences in lamb mortality attributable to the type of cross of dam and to the breed of the dam's sire, but not to the breed of the dam's dam.

Several published reports from University and Research station flocks involving different breeds, provide evidence of significant breed variation in lamb mortality; a few reports do not. From USA, Venkatachalam, Nelson, Thorp, Luecke and Gray (1949) reported highly significant variation in lamb mortality (varying from 18 to 42%) among the six breeds of the Michigan State College flock; whilst Vetter, Norton and Garrigus (1960) made a similar observation for four purebred flocks of different breeds at the University of Illinois from the records covering 37 years; Shelton's (1964) study shows differences in lamb mortality attributable to breed of sire.

Gordon (1967) reported significant differences in lambing percentages but not in lamb mortality for five breeds or crosses in Ireland. In Great Britain, Purser and Young (1959) studied factors influencing lamb mortality in two separate hill flocks and showed a Scottish Blackface flock lost 19% of lambs before weaning compared with 12% in a Welsh Mountain flock. Although this comparison was confounded with environmental differences between the farms, the ranking of these two breeds was the same in a grassland flock where both breeds were kept together (Wiener, 1967). Gunn and Robinson (1963) reported a higher mortality among South Country Cheviot lambs (16%) than among Scottish Blackface lambs (11%) on a farm in the Borders of Scotland. Donald, Read and Russell (1968) in a comparison of crossbred females produced by mating Blackface ewes to Border Leicester, Clun Forest, Dorset Horn, Finnish Landrace, and Tasmanian Merino rams noted no statistically significant breed variation in lamb mortality for three age groups of dam, but among the 1-year-old females alone, the lamb mortality of these different breed crosses varied between 14 and 29% of the lambs born. Lamb losses from swayback, occurring in this flock in one year, differed significantly among these breed crosses (Wiener, 1966).

In a number of studies crossbred sheep were compared with purebred. Donald, Read and Russell (1963) compared Blackface with Swaledale and crosses between these breeds. Losses of lambs were similar but there was evidence, short of statistical significance, that the crosses exceeded the parental mean in prolificacy. In relation to lamb mortality alone, preliminary evidence from a flock involving Blackface, Cheviot and Welsh Mountain breeds and their crosses suggests that lamb losses were lower among crossbred lambs (12%) from crossbred mothers than among purebred lambs (20%) born to purebred mothers (Wiener, 1966). In a survey of lamb mortality on agricultural research stations in Western Australia, Crocker (1968) showed that crossbred sheep kept on one station had substantially lower mortality than Merino and Corriedale kept at other research stations and concluded that the breeding system contributed to the variation in

mortality rates among the stations. Hight and Jury (1969) in a study of lamb mortality in hill country flocks in New Zealand reported that crossbred ewes (Border Leicester × Romney) produced substantially more lambs at birth and at weaning than pure Romney and that lamb survival was highest for F2 lambs from F1 ewes (86%) than for other grades of cross (F_1–F_4) or for the purebred Romney.

The published reports and the surveys of the present study support the idea that breed and breeding system influence the number of lambs weaned per ewe and its components, the lambing percentage and lamb mortality. More specific trials than the present surveys will, however, be required to show which breeds or combinations of breeds are best for particular circumstances, although the design of the Thornber survey permits limited interpretation of the results in this more specific way.

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EFFECTS OF CROSSBREEDING AND INBREEDING ON THE FREQUENCIES OF BLOOD GROUPS IN THREE BREEDS OF SHEEP

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SUMMARY

Blood groups were determined for eight loci in a total of 742 sheep and for the *Tf* (transferrin) locus of 512 sheep comprising the Scottish Blackface, the Cheviot and the Welsh Mountain breeds and their crosses. Each breed and cross was represented by a non-inbred F_2 generation and by three stages of inbreeding (25, 37½ and 50%). The loci for which all genotypes were distinguished were Hb, M, and Tf, and those for which partial description (including the recessive homozygote) was made were A, B, C, D, R and i.

There were large differences among the three pure breeds only for the frequencies at the Hb and Tf loci. The homozygote frequencies of the Blackface-Welsh and Cheviot-Welsh crosses were approximately half-way between their respective pure breeds. For the Blackface-Cheviot cross the homozygote frequency was considerably lower than either parental breed, suggesting that over all loci there were greater differences in gene frequencies between these two breeds than between the Blackface and Welsh or Cheviot and Welsh.

On average over all loci (except Tf) inbreeding had the effect of decreasing heterozygosity roughly in relation to expectation. Individually this effect was statistically significant only for *ii*, M^bM^b, Hb^AHb^A and Hb^bHb^b. For the Tf locus there was no average decrease in heterozygosity as a result of 25% inbreeding but thereafter there was a greater decrease in the purebreds than in the crosses.

There were small (<0·20) but significant residual correlations between R-O-*ii* blood types and genotypes at several other loci, and between *dd* and the M system genotypes.

INTRODUCTION

CROSSBREEDING is expected to increase the proportion of heterozygotes in a population and inbreeding to decrease it. A flock of sheep in which both mating systems were being practised gave the opportunity to observe the changes at nine blood group loci. This paper presents the results and also provides information on frequencies of the various blood types in the breeds involved.

MATERIAL AND METHODS

Animals

The breeds involved were the Scottish Blackface, the South Country Cheviot and the Welsh Mountain, and the crosses among these. After the

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purchase, in 1955, of the foundation population chosen to be representative of their breeds, an F_1 generation of crosses and contemporary purebreds (also referred to as F_1) were produced by a diallel system of mating (for details see Wiener, 1967). Thereafter an F_2 generation was produced by mating unrelated F_1 animals of the same breed or cross (pooling reciprocal crosses). Additionally each breed and crossbred type was inbred by matings of offspring by younger parent, and occasionally by full-sib matings, to produce three classes with inbreeding coefficients of 25, $37\frac{1}{2}$ and 50% (referred to hereafter as I_1, I_2 and I_3 generations).

Blood samples were taken in October 1965 and February 1966 from the 742 available sheep but only 512 of these were typed for transferrin. The generations represented were F_2, I_1, I_2 and I_3, but only some of the inbred sheep at that time were offspring of the F_2 sheep bled. Hence the gene frequencies in the inbred generations provide to some extent independent information about frequencies in the different breeds.

The animals were managed as a single flock and maintained in fields of sown pastures on the upland farm of Blythbank in Peeblesshire.

Statistical procedure

Within each of the six breed groups, animals were classified into subgroups according to inbreeding, as F_2, I_1, I_2 or I_3 so that there was a total of 24 subclasses with numbers of animals within each ranging from 3 to 66. In order to obtain estimates of marginal frequencies a least squares analysis was carried out using individual frequencies. Individuals were scored as 1 or 0 for presence or absence of a particular genotype or as frequencies 1, 0·5 or 0 for a particular allele. For comparative purposes, values for breeds are presented in terms of a constant inbreeding base, F_2; similarly, values for the inbreeding classes are given to a constant breed base, the Scottish Blackface. This procedure does not take account of possible interactions between breed and inbreeding which might occur due to differences between breeds in F_2 genotype frequencies. However it does allow simple comparisons within breeds and inbreeding groups. For some aspects of the results the effects of any interactions are considered later.

In order to assess the significance of variation attributable to breed and inbreeding group a further analysis was done using a weighted arcsin transformation of the subclass frequencies, with the intention of stabilizing the variance. The frequency of the type treated last in each blood group system was obtained by difference and no separate statement of significance of variation of that type can therefore be made.

Breed and inbreeding means from both the transformed and untransformed analyses were calculated but only the latter are presented in the Tables to avoid the possible introduction of bias in back transforming extreme values (*see* Finney, 1973). For intermediate frequencies, 0·1–0·8, the results were virtually identical.

Residual correlations between genotype frequencies were obtained from the initial least squares analysis on untransformed data and significance levels quoted in the results refer to this analysis, however these should only be interpreted with caution, as the data do not satisfy some of the implicit assumptions of such analysis.

The goodness of fit of the frequencies of genotypes in the F_2 generation in relation to Hardy-Weinberg expectations was tested by chi-square.

Blood-typing procedure

Antigenic factors of the red blood cells were determined using standard serological tests (Rasmusen, 1962). The nomenclature used is that decided upon at the workshop of the International Society of Animal Blood Group Research on Blood Typing in Sheep held at Jouy-en-Josas, France, in 1973. The equivalence of this nomenclature to that used by Rasmusen (1962) is: A = Aa; P = Ba; B′ = Bb; O′ = Bg; S = Bh; C = Ca; C_x = Cb; D = Da; M_x = Ma; R, O and *ii* remain unchanged.

Potassium type. Whole heparinized blood diluted 1 in 201 was estimated for potassium in an EEL flame photometer. Animals with values of 40 m equiv K per litre of erythrocytes and below were classified as low (LK), others as high (HK).

Haemoglobin type. This was determined by starch gel electrophoresis (Starch-Hydrolysed from Connaught Medical Research Laboratories, University of Toronto, Canada), in a continuous Tris-EDTA-boric acid buffer at pH 8·6. The faster migrating haemoglobin was recorded as A, the slower as B, no variants were seen.

Transferrin type. This was determined by starch gel electrophoresis in a discontinuous buffer system with Tris-citrate buffer at pH 7·6–7·7 and boric acid-sodium hydroxide electrolyte at pH 7·6–8·0. The notation of A, B, C, D, E is described by Cooper, Bailey and Mayo (1967). Transferrins now labelled G and M may have been present but undetected. Homozygotes AA and DD in *Results* may therefore have included G and M respectively in the heterozygous condition.

Notation. Genotypic classifications used in this paper are A^a- versus *aa* (absence of factor Aa); *B*- versus *bb* (absence of Ba, Bb, Bg and Bh, where both the 'dominant' and 'recessive' types are known to include more than one genotype, which may be identified by tests using reagents for additional factors in the B system); C^{ab}- versus C^b- versus *cc* (absence of factors Ca and Cb; in these sheep Ca never occurred without Cb so there is no C^a- class); D^a- versus *dd* (absence of Da); M^aM^a versus M^aM^b versus M^bM^b (where presence of factor Mb is inferred from blood potassium determinations, with M^aM^a responsible for the HK or high-potassium type and M^aM^b and M^bM^b for the LK or low-potassium type) Tucker, 1971; and R versus O versus *ii*. Type R is genotypically *R-I-* and O is r^or^oI- as a result of epistatic interaction of alleles at the R and I loci (*see* review by Rasmusen, 1962).

RESULTS

Frequencies among breeds

Table 1 shows adjusted frequencies of the genotypes found at the A, B, C, D, i, M and Hb loci and R and O types in the different breeds and crosses. For each of the three pure breeds the commonest type at each locus was A^a-, *B*-, C^b-, *dd*, O and M^aM^b. Only at the Hb locus did the allele at higher frequency differ among breeds. For the Blackface the descending order of frequency was Hb^AHb^A, Hb^AHb^B, Hb^BHb^B while for the Cheviot and the Welsh it was Hb^AHb^B, Hb^BHb^B, Hb^AHb^A. Variation in frequency among the breeds and crosses was significant for the types *aa*, C^{ab}-, *dd*, *ii*, O, M^aM^a, Hb^AHb^A and Hb^BHb^B.

An interesting aspect of these results lies in considering how genetically similar or different the pure breeds are. A measure of this can be obtained

TABLE 1

The frequencies of blood group genotypes and alleles in three breeds of sheep and their crosses†

	Breed or cross‡						
Number of animals	B 79	C 70	W 119	B×C 152	B×W 178	C×W 144	Significance of variation§
Blood type							
aa	0·29	0·42	0·32	0·28	0·48	0·43	0·02
A^a-	0·71	0·58	0·68	0·72	0·52	0·57	—
bb	0·17	0·47	0·35	0·28	0·37	0·30	0·22
B-	0·83	0·53	0·65	0·72	0·63	0·70	—
cc	0·17	0·31	0·11	0·16	0·19	0·25	0·08
C^{ab}-	0·19	0·03	0·03	0·43	0·06	0·00	<0·01
C^b-	0·64	0·66	0·86	0·41	0·75	0·75	—
dd	0·76	0·61	0·59	0·46	0·67	0·52	0·01
D^a-	0·24	0·39	0·41	0·54	0·33	0·48	—
ii	0·14	0·00	0·03	0·17	0·10	0·06	0·03
O	0·70	0·72	0·80	0·55	0·49	0·60	<0·01
R	0·16	0·28	0·17	0·28	0·41	0·34	—
M^bM^b	0·11	0·14	0·10	0·04	0·00	0·16	0·06
M^aM^a	0·37	0·36	0·43	0·39	0·63	0·34	<0·01
M^aM^b	0·52	0·50	0·47	0·67	0·37	0·50	—
Hb^AHb^A	0·57	0·00	0·16	0·13	0·18	0·03	<0·01
Hb^BHb^B	0·02	0·43	0·29	0·35	0·12	0·46	<0·01
Hb^AHb^B	0·41	0·57	0·55	0·52	0·70	0·51	—
Alleles							
M^b	0·37	0·39	0·33	0·33	0·18	0·41	0·01
M^a	0·63	0·61	0·67	0·67	0·82	0·59	—
Hb^A	0·78	0·28	0·43	0·39	0·53	0·28	<0·01
Hb^B	0·22	0·72	0·57	0·61	0·47	0·72	—

† Given in terms of F_2 animals as a base.
‡ See footnote to Figure 1 for notation.
§ Analysed using a weighted arcsin transformation of subclass frequencies to stabilize the variance.

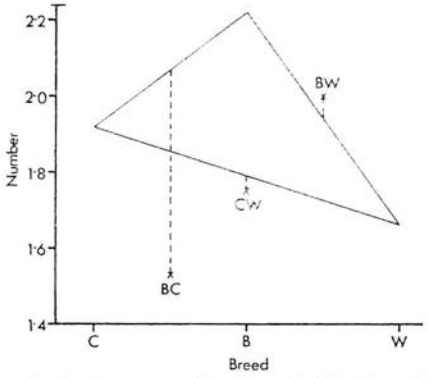

Fig. 1. Number of recessive homozygotes for seven loci in three breeds and their crosses.

B = Blackface B×C = Blackface×Cheviot cross
C = Cheviot B×W = Blackface×Welsh cross
W = Welsh C×W = Cheviot×Welsh cross

The values for the three pure breeds are joined to form a triangle so that each crossbred value can be shown in relation to average for the pure breeds involved.

by comparing the general level of homozygosity of the crossbreds with that of the pure breeds involved. This has been done by calculating for each individual the number of homozygous recessive loci it carried. (Throughout, the homozygous types M^bM^b and Hb^AHb^A have been treated as recessive in order to combine the data with that for loci for which only one homozygous type was identified.) The results of this are shown in Figure 1. The Blackface

TABLE 2

The frequencies of transferrin types and alleles at the Tf locus in three breeds of sheep and their crosses†

	Breed or cross‡						
	B	C	W	B×C	B×W	C×W	Significance
Number of animals	65	48	75	106	117	101	of variation§
Type							
AA	0·00	0·07	0·09	0·00	0·00	0·04	0·04
AB	0·02	0·11	0·10	0·17	0·04	0·05	<0·01
AC	0·00	0·16	0·13	0·03	0·03	0·19	<0·01
AD	0·08	0·08	0·19	0·07	0·05	0·05	0·03
BB	0·29	0·01	0·04	0·16	0·13	0·11	<0·01
BC	0·03	0·13	0·13	0·15	0·13	0·13	0·12
BD	0·13	0·03	0·12	0·18	0·28	0·10	<0·01
CC	0·00	0·33	0·00	0·03	0·00	0·19	<0·01
CD	0·04	0·07	0·10	0·15	0·12	0·14	0·12
DD	0·41	0·00	0·07	0·06	0·20	0·00	<0·01
DE	0·00	0·01	0·03	0·00	0·02	0·00	—
Alleles							
Tf^A	0·03	0·25	0·30	0·13	0·06	0·18	<0·01
Tf^B	0·40	0·14	0·21	0·42	0·35	0·25	<0·01
Tf^C	0·01	0·52	0·18	0·19	0·14	0·43	<0·01
Tf^D	0·56	0·08	0·30	0·26	0·44	0·14	<0·01
Tf^E	0·00	0·01	0·01	0·00	0·01	0·00	—

† Given in terms of F_2 animals as a base.
‡ See Fig. 1.
§ See Table 1.

were the most homozygous pure breed and the Welsh the least, with the Cheviot lying midway. The Blackface-Cheviot cross had a very low number of homozygous loci and in this respect was very different from the mean of the pure breeds involved, indicating genetic dissimilarity of these two pure breeds. For the other two crosses the number of homozygous loci was similar to the mean of that for the parental breeds.

Table 2 gives the frequencies, in the breed groups, of genotypes and genes at the transferrin locus for the 512 animals which were typed. Variation due to breed was significant for the frequency of all the alleles and most of the genotypes. The Figures show that Blackface had the alleles Tf^B and Tf^D at the highest frequency while the Cheviots had the alleles Tf^A and Tf^C at the highest frequency. The Welsh had Tf^A and Tf^D at the highest frequency but also had fairly high frequencies of $Tf^B$and Tf^C. The Tf^E allele was found only in the Tf^D Tf^E genotype for which there were only three individuals. In terms of the transferrin locus it can be said that the Blackface and Cheviot were the more dissimilar of the pure breeds while the Welsh held an intermediate position. This observation is illustrated in Figure 2 which shows the

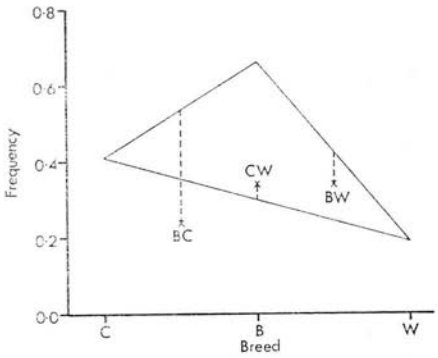

FIG. 2. Frequency of homozygotes at the Tf locus in three breeds and their crosses.

B = Blackface
C = Cheviot
W = Welsh
B × C = Blackface × Cheviot cross
B × W = Blackface × Welsh cross
C × W = Cheviot × Welsh cross

The values for the three pure breeds are joined to form a triangle so that each crossbred value can be shown in relation to the average for the pure breeds involved.

relationships of the crosses to the purebreds in the overall frequency of homozygotes at the transferrin locus.

For the Hb, M and Tf loci both heterozygous and homozygous genotypes could be distinguished. Table 3 shows that for the F_2 generation, pooled over breeds, only in the case of Hb were there significantly more heterozygous genotypes (Hb^AHb^B) than expected on the assumption of Hardy-Weinberg equilibrium. The apparent excess of M^aM^b was not significant, and for

TABLE 3

Comparison of the observed number of animals of each Hb, M and Tf genotype in the F_2 generation with those expected under Hardy-Weinberg equilibrium†

Locus	Genotype	Numbers		d.f.	χ^2
		Observed	Expected		
Hb	Hb^AHb^A	30	40·6		
	Hb^AHb^B	109	87·8		
	Hb^BHb^B	56	66·6	2	9·57*
M	M^aM^a	86	92·7		
	M^aM^b	93	80·2		
	M^bM^b	16	22·1	2	4·21
Tf	Tf^ATf^A	3	3·7		
	Tf^ATf^B	11	12·0		
	Tf^ATf^C	12	10·3		
	Tf^ATf^D	11	11·9		
	Tf^BTf^B	17	14·7		
	Tf^BTf^C	16	15·1		
	Tf^BTf^D	21	26·3		
	Tf^CTf^C	10	11·4		
	Tf^CTf^D	15	14·2		
	Tf^DTf^D	16	14·0	9	2·51

† Expectations calculated within each breed and pooled over breeds.
* χ^2 significant at 5% level.

the Tf locus the observed deviations in frequency from expectation were trivial overall. The biggest deviation was given by Tf^BTf^D, which was most marked in the Blackface breed.

Effects of inbreeding

Table 4 shows the frequencies of the homozygous genotypes for the F_2 group and the three inbred groups. In all cases, except M^aM^a, there was an overall increase in frequency from F_2 to I_3 although the variation among the groups was significant only for the genotypes *ii*, M^bM^b, Hb^AHb^A and

TABLE 4

The effect of inbreeding on the frequency of homozygous blood group loci†

	Inbreeding group				Significance of variation‡
	F_2	I_1	I_2	I_3	
Inbreeding coefficient	0·000	0·250	0·375	0·500	
Number of animals	195	287	216	44	
Recessive genotype†					
aa	0·29	0·32	0·34	0·32	0·85
bb	0·17	0·21	0·24	0·32	0·67
cc	0·17	0·21	0·25	0·27	0·20
dd	0·76	0·78	0·81	0·77	0·79
ii	0·14	0·22	0·31	0·35	<0·01
M^bM^b	0·11	0·19	0·29	0·58	<0·01
Hb^AHb^A	0·57	0·67	0·75	0·79	<0·01
Total number of recessive homozygotes	2·21	2·60	2·99	3·42	<0·01
Other genotypes					
M^aM^a	0·37	0·45	0·43	0·28	0·15
Hb^BHb^B	0·02	0·15	0·13	0·13	<0·01

† Given in terms of the Scottish Blackface as a base.
‡ See Table 1.
§ The M^bM^b and Hb^AHb^A genotypes are not recessive but are treated as if they are in order to include data for the M and Hb loci.

Hb^BHb^B where the increase with inbreeding was considerable. An overall measure of homozygosity was given by the number of recessive homozygous loci which increased from 2·2 to 3·4 with inbreeding. Table 5 indicates how the total number of homozygous recessive loci changed with inbreeding within each breed compared with expectation. The calculations of changes expected to be produced due to inbreeding were made within each locus and each breed, and take account of the possibility of breed × inbreeding interactions. These calculations were based on the assumption of initial Hardy-Weinberg equilibrium, and the absence of change in gene-frequencies due to selection and to sampling. For the crossbred groups the calculation of expectations required some adjustment since the F_2 and I_1 generations were derived from a group (F_1) which was not itself in equilibrium. In general the increasing frequency of the recessive homozygotes, and presumably the corresponding decrease in heterozygotes, agreed with expectation.

The effect of inbreeding on the frequencies of genotypes at the transferrin

TABLE 5

The total number of 'recessive' homozygotes for each breed × inbreeding group compared with expectation.† (Number of animals in each subclass shown in parentheses)

		Inbreeding group					
		I_1		I_2		I_3	
	F_2 O	O	E	O	E	O	E
Blackface	2·32 (19)	2·47 (36)	2·69	3·05 (21)	2·87	4·00 (3)	3·05
Cheviot	2·18 (17)	2·36 (33)	2·27	2·40 (15)	2·46	2·80 (5)	2·55
Welsh	1·42 (28)	2·13 (46)	1·70	2·50 (42)	1·84	3·00 (3)	1·97
B × C	1·88 (41)	1·86 (56)	2·17	2·15 (48)	2·41	2·29 (7)	2·62
B × W	1·94 (47)	2·51 (66)	2·23	2·86 (55)	2·44	2·20 (10)	2·62
C × W	1·49 (43)	2·02 (50)	1·65	2·66 (35)	2·00	3·75 (16)	2·21

† Expected numbers of recessive homozygotes calculated by assuming that each step of inbreeding reduces the heterozygote frequency, estimated in the F_2, by a proportion equal to the inbreeding coefficient, with adjustments for crossbreds as noted in the text.

TABLE 6

The effect of inbreeding on the frequency of homozygous and heterozygous transferrin types†

		Inbreeding group			
	F_2	I_1	I^2	I_3	Significance
Inbreeding coefficient	0·000	0·250	0·375	0·500	of variation‡
Number of animals	133	182	165	32	
Homozygous types					
AA	−0·03	−0·01	0·03	0·08	0·07
BB	0·30	0·29	0·29	0·30	1·00
CC	−0·04	−0·01	0·04	0·14	<0·01
DD	0·42	0·44	0·48	0·49	0·30
Heterozygous types					
AB	0·03	−0·01	−0·01	−0·02	0·10
AC	0·00	0·00	0·00	−0·05	0·97
AD	0·09	0·12	0·05	0·08	0·06
BC	0·04	0·00	0·01	−0·02	0·65
BD	0·14	0·16	0·10	0·05	0·11
CD	0·05	0·01	0·00	−0·04	0·45
DE	−0·01	0·01	0·01	−0·01	—
Overall frequencies					
Homozygous types	0·66	0·71	0·84	1·01	0·01
Heterozygous types	0·34	0·29	0·16	−0·01	—

† Given in terms of the Scottish Blackface as a base.
‡ See Table 1.

locus can be seen from Table 6. For the individual genotypes only one, the CC homozygote, showed a significant change with inbreeding. A more useful measure of the effect of inbreeding is given by the change in overall frequency of transferrin homozygotes which increased significantly with inbreeding as shown at the foot of Table 6.

The effect of inbreeding on the frequencies of homozygous Tf genotypes can be seen separately for each breed in Table 7 compared with expectations

TABLE 7

The overall frequency of homozygous transferrin types for each breed × inbreeding group compared with expectations. (Number of animals in each subclass shown in parentheses)

		Inbreeding group					
	F_2	I_1		I_2		I_3	
	O	O	E	O	E	O	E
Blackface	0·76 (17)	0·63 (30)	0·82	0·87 (16)	0·85	1·00 (2)	0·88
Cheviot	0·38 (13)	0·40 (20)	0·53	0·67 (12)	0·61	1·00 (3)	0·69
Welsh	0·15 (20)	0·13 (23)	0·36	0·47 (30)	0·47	1·00 (2)	0·57
B×C	0·28 (25)	0·33 (39)	0·39	0·40 (35)	0·51	0·29 (7)	0·60
B×W	0·40 (30)	0·39 (36)	0·45	0·48 (44)	0·57	0·71 (7)	0·65
C×W	0·21 (28)	0·53 (34)	0·31	0·46 (28)	0·46	0·73 (11)	0·56

† Expected frequencies calculated by assuming that each step of inbreeding reduces the heterozygote frequency, observed in the F_2, by a proportion equal to the inbreeding coefficient, with adjustments for crossbreds as noted in the text.

which were calculated within each breed. Of the three pure breeds none increased in the frequency of homozygous Tf genotypes with the first step of inbreeding; thereafter, however, the increase in homozygosity reached or exceeded expectation, and the few 50% inbred animals were all homozygous. Blackface-Cheviot crosses appeared to 'resist' fixation at this locus, as did Blackface-Welsh crosses up to the I_2 stage and only the Cheviot-Welsh crosses had increased in the frequency of homozygotes more than expected at the I_1 stage and at I_3.

Correlations between blood group loci

After taking account of breed and inbreeding effects as in the initial least squares analysis, residual correlations were calculated among the frequencies of the various homozygous recessive genotypes at the A, B, C, D, R, i, M and Hb loci. From Table 8 it can be seen that of the 21 correlations only 5 were statistically significant (see section on statistical procedure) and none was any higher than 0·2. Three of the significant correlations involved the R-O system and the relationship of the system as a whole with the A, B, C

and Hb locus is shown in the first part of Table 9. Types in excess were *aaii*, *bbii*, *ccii*, *bb* O and Hb^AHb^A O while those with a deficiency were *aa* O, *cc* O and C^{ab}-*ii*. The second part of Table 9 shows the residual correlations between *dd* and the M system. This suggests an excess of *dd* M^aM^a genotypes and a deficiency of *dd* M^bM^b genotypes. Unfortunately insufficient suitable family data were available to test for possible linkage of these systems.

TABLE 8

Residual correlations (after taking account of breed and inbreeding effects) between the frequencies of homozygous 'recessive' genotypes

	aa	*bb*	*cc*	*dd*	*ii*	M^bM^b	Hb^AHb^A
aa	1·00						
bb	0·08*	1·00					
cc	−0·01	0·06	1·00				
dd	−0·05	−0·02	0·04	1·00			
ii	0·10*	0·10*	0·17*	0·02	1·00		
M^bM^b	−0·05	−0·04	−0·02	−0·20*	0·06	1·00	
Hb^AHb^A	−0·02	0·00	−0·00	−0·01	−0·03	−0·02	1·00

* Correlations significant at 5% level (see Statistical procedures section).

TABLE 9

Residual correlations

(*a*) Between the genotypes *aa*, *bb*, *cc*, C^{ab}- and Hb^AHb^A and the types *ii* and O

	aa	*bb*	*cc*	C^{ab}-	Hb^AHb^A
ii	0·10*	0·10*	0·17*	−0·07*	−0·03
O	−0·07*	0·09*	−0·09*	0·04	0·14*

(*b*) Between the genotype *dd* and the genotypes M^bM^b and M^aM^a

	dd
M^bM^b	−0·20*
M^aM^a	0·15*

* Correlations significant at 5% level (see Statistical procedures section).

DISCUSSION

A number of factors invite caution in the interpretation of the results. Since only about two-thirds of the inbred animals were descended from the F_2 animals sampled at the same time, the best estimate of gene frequencies in the different breeds should not be based on values derived from the F_2 generation alone. The inbreds provide partially independent information about frequencies in these breeds as long as interactions between breed and degree of inbreeding can be ignored. For the same reason, changes in frequencies of homozygotes with inbreeding compared with the frequencies at the F_2 stage may include more than the usual element of sampling variation. Another reservation, not unusual in animal blood group data, arises from the difficulty of estimating expected frequencies when not all genotypes are distinguished. The necessary assumptions of Hardy-Weinberg equilibrium may not be correct and cannot be tested.

With these reservations the results suggest that the frequencies of the alleles in the A, C and D systems shown in Table 1 are within the ranges of those reported for other breeds, although the variation in the frequencies of

R and O appears to be less (Rasmusen, Stormont and Suzuki, 1960; Stansfield, Bradford, Stormont and Blackwell, 1964; Stormont, Suzuki, Bradford and King, 1968).

For the M system (frequently described only in terms of high or low blood potassium) and the Tf and Hb loci wide variations in frequencies are to be found in other reports (*see* Agar, Evans and Roberts, 1972; Stormont *et al.*, 1968). Explanations based on adaptation to particular environments have been put forward but the present data are not suitable to test such hypotheses.

Comparison of the frequency of homozygotes in the crossbreds and in the parental purebreds gives some indication of the general genetic similarity of the breeds involved. Figures 1 and 2 show that both for the total number of recessive homozygotes and for the transferrin homozygotes only the Blackface × Cheviot cross had a frequency which was very different from the midparent level. For the transferrin homozygotes this was expected from the very different allele frequencies in the two breeds as seen in Table 2. However, for the recessive loci this apparent dissimilarity is not immediately obvious from Table 1 although it can be deduced if assumptions of Hardy-Weinberg equilibrium are made. The Figures 1 and 2 also agree in ranking of the pure breeds.

The data on the effect of inbreeding (Table 4) indicate that at four loci the recessive genotypes did not increase significantly in frequency with increasing inbreeding but at the three others they did so quite markedly. Unfortunately the estimates of expected changes at individual loci, particularly for those where all genotypes were not defined, cannot be made sufficiently well to decide whether the different responses to inbreeding at different loci have biological significance. It is possible that some form of selection may have operated to oppose or enhance the effects of inbreeding but the data are not suitable for testing this. However, in the M system one of the homozygotes M^aM^a showed at first no change and then an unexpected drop in frequency at the I_3 stage of inbreeding. This may indicate selection for the M^bM^b homozygote which increased markedly in frequency with inbreeding. The increase in the frequency of Hb^BHb^B homozygotes corresponded to that in Hb^AHb^A. For the Tf locus (Table 6) the average changes corresponded to expectation within the limits of sampling error. The difference between the purebreds and crossbreds (Table 7) however, is noteworthy. The 'resistance' to the loss of heterozygosity, common to all except the Cheviot-Welsh cross, as a result of the first stage of inbreeding was not maintained for the pure breeds at later stages but continued for two of the three crosses. Whilst heterozygotes may therefore have been at a selective advantage the difference between the crosses and the purebreds at the Tf locus is difficult to explain in these terms. However, it is pertinent to note that in respect of a number of performance traits in the same flock Wiener and Hayter (unpublished) have observed that, contrary to expectation, the performance of the crossbred sheep declined on average less rapidly than that of the purebreds when both types were inbred.

The significant residual correlations involving *ii* and O suggest the possible importance of the R-O-*ii* types in maintaining balanced polymorphisms for blood group loci. The correlation of *ii* with C^{ab}- and *cc* may be due to the reported close linkage between the I and C loci (Rasmusen, 1966). On the other hand, even the significant correlations were very low, suggesting that

practically all (>96%) the variation at one locus was independent of that at others.

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BODY SIZE AND CONFORMATION IN SHEEP FROM BIRTH TO MATURITY AS AFFECTED BY BREED, CROSSBREEDING, MATERNAL AND OTHER FACTORS

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SUMMARY

Body weight was studied from birth to 5½ years of age and six linear measures of body size from birth to 4¼ years for sheep of five breeds, Scottish Blackface, Cheviot, Welsh Mountain, Lincoln Longwool and Southdown, and of crosses of these breeds with each other and with the Tasmanian Merino, but not in all possible combinations. The sheep were run as a single flock. Numbers ranged from 753 at birth to 150 at the end of the experimental period.

There were marked differences among the breeds and crosses in all aspects of body size and some differences in rate of maturity. They also differed in conformation independently of body weight.

Crosses of the hill breeds with the Lincoln and probably with the Southdown were heavier than the average of the parental breeds and larger in some linear body measurements from about weaning onwards. The weights of crosses of Blackface and Cheviot with Lincoln eventually exceeded those of the heavier parent of the cross. For the crosses among the three hill breeds only the Blackface-Cheviot cross showed significant deviations from mid-parent values for weight and size.

Maternal effects were important for all traits studied from birth to weaning and for weight up to a year old. In relation to mature size, Welsh dams produced the biggest and Lincoln the smallest lambs. The data did not permit Southdown maternal effects to be estimated.

The effects of birth type and rearing were apparent for late maturing body parts up to a year old and for weight up to 3 years. Males, measured only from birth to weaning, were heavier and generally larger than females.

Residual correlations between the various measures of size varied from 0·1 to 0·7.

INTRODUCTION

THE aim of this paper is to provide comparisons of growth in body weight and linear measures of size of five pure breeds together with their crossbreds when they were run together as a single flock from birth onward. The observations taken at regular and frequent intervals continued for a proportion of the sheep until they were 5½ years old thus ensuring not merely an unusually extensive

body of data on variations in growth but reasonably reliable estimates of mature size.

Crossbreeding systems are intended not infrequently to combine distinct virtues of the sire and dam lines. Separate estimates of the effects of breed and maternal environment on lamb growth are then desirable and the present experiment provides these as well as estimates of heterosis. Various aspects of the performance, including growth, of the animals which formed the foundation population of this flock (the parents of the animals considered in this paper) were described by Wiener (1967).

MATERIAL AND METHODS

Animals. Details of the foundation flock were given by Wiener (1967) and are outlined here. Female sheep of the Scottish Blackface (Blackface), Cheviot, Welsh Mountain (Welsh), Lincoln Longwool (Lincoln) and Southdown breeds were purchased in 1955 when they were approximately 5 months old. Each breed (except Southdown) was obtained from a variety of sources. These ewes and the subsequent generations were managed as a single flock throughout their life and were kept on a grassland farm (elevation around 300 m) at Blythbank in Peeblesshire, Scotland.

Supplementary feed (hay and concentrates) was offered only during periods of prolonged snow and for about 6 weeks prior to lambing.

Blackface, Cheviot, Welsh, Lincoln, Southdown and Tasmanian Merino (Merino) rams were obtained from a variety of flocks (2 rams each year for 3 years for the first 4 breeds, and 2 each year for 2 years for the last 2 breeds) and each ram was used only in one year. The number of foundation females and pattern of matings involved in producing the first generation of progeny, the animals under discussion in the present study, are shown in Table 1. Each foundation female was mated to a different breed of ram each year;

TABLE 1

Pattern of matings producing the first generation (F_1) animals

Breed of dam	Approx. no. of females mated each year	Breed of sire					
		B	C	W	L	S	M†
Scottish Blackface (B)	74	3‡	3	3	2	2	2
Cheviot (C)	74	3	3	3	2	2	2
Welsh Mountain (W)	70	3	3	3	3	2	2
Lincoln Longwool (L)	24	0	0	3	3	0	0
Southdown (S)	12	0	0	0	0	2	0

† Merino.
‡ Number of years that type of mating was made.

Table 1 shows the number of years that each type of mating was made.

Measurements. Sheep were weighed to the nearest 0·1 lb at birth and to the nearest 1 lb subsequently. (Units were converted to kg for the purposes of this paper.)

Measurements of the following six linear body dimensions were made to the nearest 0·1 cm using calipers.

Body length—from the anterior point of the shoulder (tuberosity of the humerus) to the posterior extremity of the pin bone (tuber ischii).

Shoulder width—the horizontal plane at the widest point over the *infraspinatus* muscle.

Hook width—the extreme width of pelvis over the tuber coxae.

Head width—maximum width at the supra-orbital processes.

Tibia length—measured on right hind leg along the anterior surface.

Cannon bone length—measured on right foreleg along the anterior surface.

Five observers were involved in taking these measurements.

Weights were taken every 3 weeks from birth to weaning (at 15 weeks of age) and body dimensions every 6 weeks from 6 weeks of age (and from birth for cannon bone length) until weaning for all lambs surviving to weaning. Weights (every 3 weeks) were then continued until 75 weeks of age and measurements (every 6 weeks) to 72 weeks for the females of the breeds and crosses involving the Lincoln, Southdown and Merino, and until 222 weeks for the females of the Blackface, Cheviot and Welsh breeds and the crosses among them. All surviving animals except the very few which had remained barren for three successive lambings continued in the flock for another year and were weighed at 3-weekly intervals until 282 weeks of age, although the measuring was terminated.

Statistical analysis. An initial analysis was undertaken to determine the magnitude and importance of observer differences in the measurement of body dimensions. Interactions between observer and age of animal and observer and breed were fitted but only the first was found to be significant. Accordingly adjustments were calculated for each observer at each age and these were used to standardize the data with respect to observer before subsequent analyses were undertaken.

The analysis took the form of fitting a linear model by the method of least squares with parameters representing the effects of: pure breed or cross of animal, maternal effect, birth type and rearing, age of dam (which is confounded with the year of birth of animal, and sires), week of birth of animal and the individual sire used within year and breed. These were all found to have a significant effect on weights or dimensions at some stage in the animal's life and were retained in the model throughout. At birth animals not surviving to weaning were included but the data were adjusted to live lambs. Sex was also fitted where appropriate (i.e. birth to weaning). Because individual sires could only be compared within breed and within year it was necessary to include the sire breed × year interaction irrespective of its statistical significance. No other interaction terms were included. As each breed of dam, except Southdown, was mated to more than one breed of sire, it was possible to estimate the maternal effect (maternal breed environment for the lamb) by fitting for maternal breed simultaneously with breed or cross of lamb (reciprocal crosses pooled), the latter already containing the genetic contribution of the maternal breed. The estimate of maternal effect for the Lincoln is not as valid as for the three hill breeds since the number of sire breeds used and the total number of matings were fewer.

Since not all pure breed or crossbred groups were kept for an equal length of time and the diallel design was 'complete' only in respect of the

three hill breeds, two sets of analyses were carried out and included the following animals:

1. *The BCW analyses*

This set included all animals of the Blackface (B), Cheviot (C) and Welsh (W) breeds and the crosses among these. They were born in the years 1957, 1958 and 1959. This set was broken down as follows:

(i) weight and cannon bone length for all animals recorded at birth, $n = 546$
(ii) weights and measurements from birth to weaning for all animals surviving to weaning, $n = 459$
(iii) weights and measurements from 18 to 75 weeks for all female animals present to 75 weeks, $n = 191$
(iv) weights and measurements from 78 to 150 weeks for all female animals surviving to 150 weeks, $n = 182$
(v) weights and measurements from 153 to 222 weeks for all female animals surviving to 222 weeks, $n = 163$
(vi) weights only from 225 to 282 weeks for all female animals surviving to 282 weeks, $n = 150$.

2. *The 'all breeds' analyses*

This set included all animals involving the Lincoln (L), Southdown (S) and Merino (M) breeds which were born in the years 1957 and 1958, in addition to the BCW breeds which were also born in those years; all animals born in 1959 were excluded. This meant that a small number of Lincoln × Welsh and pure Lincoln animals born in 1959 were omitted entirely. This set was broken down as follows:

(i) weight and cannon bone length for all animals recorded at birth, $n = 753$
(ii) weights and measurements from birth to weaning for all animals surviving to weaning, $n = 647$
(iii) weights and measurements from 18 to 75 weeks for all female animals present to 75 weeks, $n = 259$.

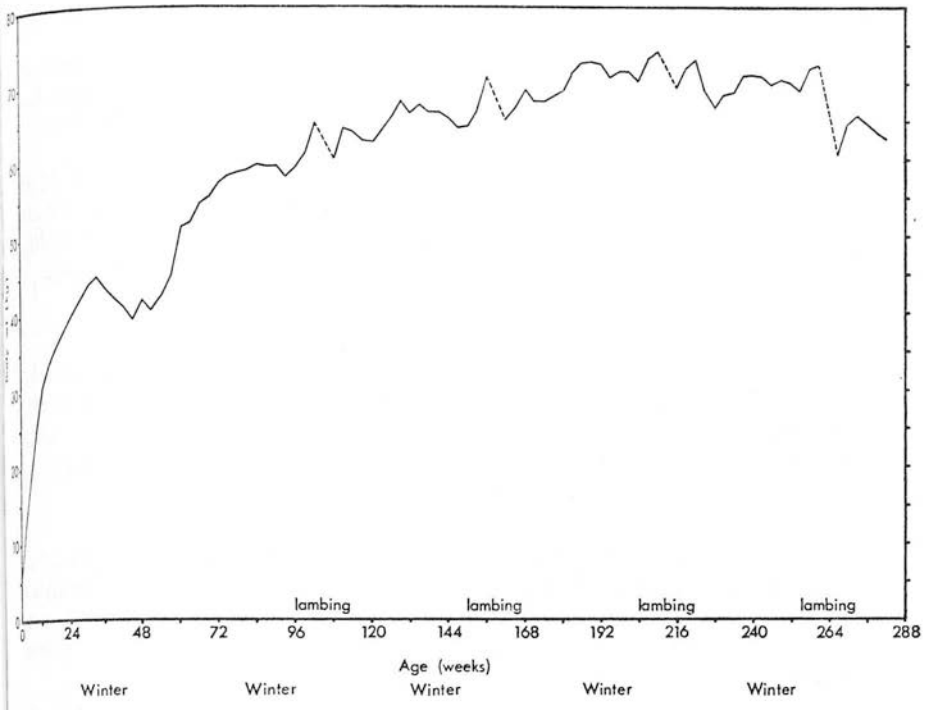
After making allowance for the effects of the various factors such as breed or cross, birth type etc., residual correlations among all pairs of measurements at each age were calculated in addition to residual correlations among the same measurements at successive ages. Residual correlations of dam's weight at 21 months and animal's weight from birth to two years were also calculated.

RESULTS

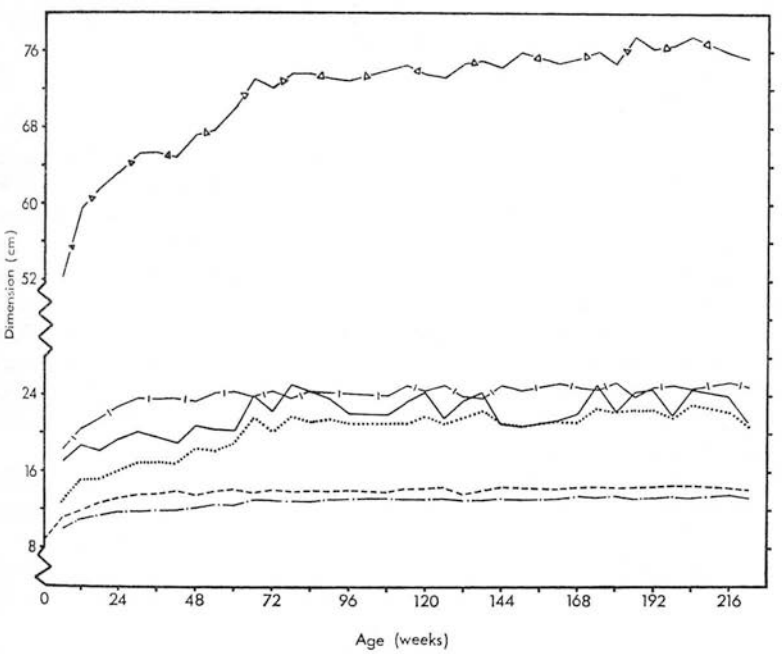
Pattern of growth

Figure 1, based on the BCW analysis, shows the pattern of growth for female Blackface animals born as singles to 2-year-old Blackface dams in an average week of lambing in 1957, and reared as singles (the fitted base class). The pattern based on the 'all breeds' analysis was very similar.

After an initial period of rapid growth and a fall in weight in the first winter, later growth in weight was marked by seasonal fluctuations. Ninety per cent of mature weight was not reached until nearly $2\frac{1}{2}$ years of age.



1a



1b

FIG. 1. Growth of (*a*) body weight from birth to 5½ years and (*b*) six linear dimensions from birth or 6 weeks to 4¾ years of sheep of the fitted base class (Scottish Blackface females born as singles to 2-year-old Blackface dams in an average week of lambing in 1957 and reared as singles). (*a*) body weight (kg) (*b*) linear dimensions (cm): body length —△—△—; shoulder width ————; hook width ·····; head width — · — · —; tibia length — | — | —; cannon bone length - - - - - - - - -.

Figure 1b shows the change in linear body dimensions with age. As expected, none showed the obvious seasonal pattern of growth seen for weight, but both for shoulder width and hook width some seasonal trends can be seen.

The body dimensions differed in their rate of maturity such that 90% of mature size was reached before 6 months of age for cannon bone and tibia length, in around 10 to 11 months for head width and shoulder width, followed by body length (13 months) and hook width (14 to 15 months).

Breed differences

Differences among the pure breeds and crosses (with reciprocal crosses pooled where appropriate) have been considered after first removing any effect attributable to maternal environment. All breeds of dam had more than one type of lamb with the exception of the Southdown where, therefore, the maternal effect cannot be removed.

Body weight. Differences among breeds and crosses are presented graphically in Figure 2. The first part (2a) uses data from the BCW analyses and shows the deviations of these breeds and crosses from Blackface, as a proportion of the fitted base. The six breed types appear to fall into three groups:

(i) the Blackface, Cheviot and Blackface-Cheviot which were consistently the heaviest,
(ii) the Blackface-Welsh and Cheviot-Welsh crosses which were on average 10 to 15% lighter than Blackface,
(iii) the pure Welsh which were on average 20 to 25% lighter than Blackface.

Although these groups remained distinct throughout the period from birth to 5½ years the variation both within and between groups increased appreciably over the first 18 months of life. Within the first group the Cheviot appeared to show more seasonal variation, gaining more weight in summer and losing more in winter, than either the Blackface or Blackface-Cheviot.

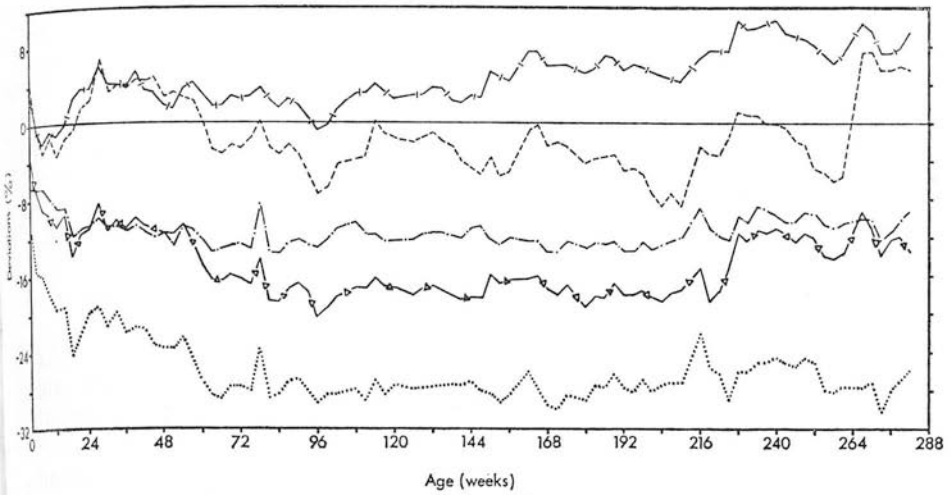
The Blackface-Welsh and Cheviot-Welsh crosses, were initially some 5% below the Blackface and this had become 15% below by 18 months. During the first year both crosses had the same body weight but during the second summer the Cheviot-Welsh did not gain as much weight and this small difference (approximately 4%) was maintained thereafter reflecting a similar difference to that between the pure Cheviot and Blackface breeds.

The Welsh breed dropped from being 11% below Blackface at birth to 26% below at 18 months, after this the difference remained fairly constant.

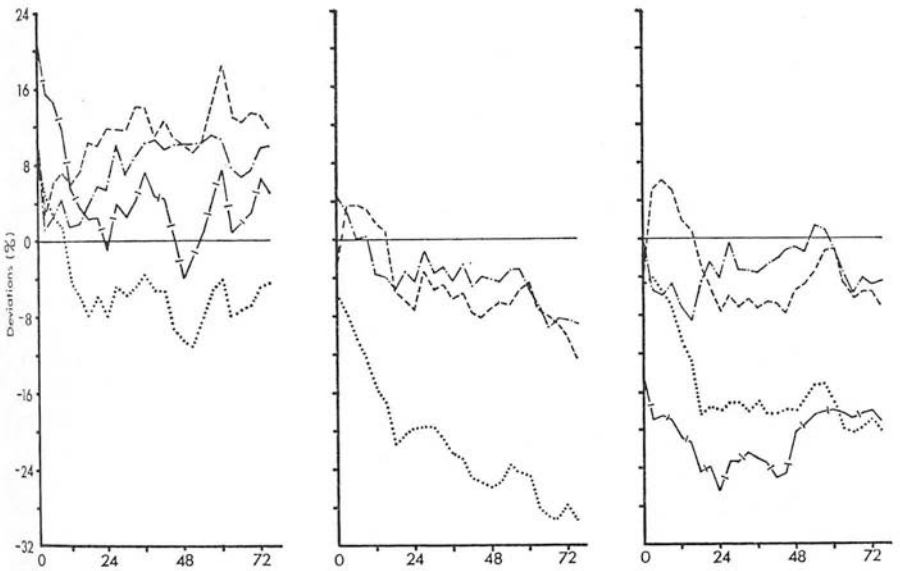
Figures 2b, 2c and 2d use data from the 'all-breeds' analyses and show the deviations of the breeds and crosses involving Lincoln (2b), Merino (2c) and Southdown (2d), from Blackface as a proportion of the fitted base. In this case the time scale is from birth to 75 weeks of age.

The Lincoln and their crosses with Blackface and Cheviot were heavier than Blackface and the Lincoln-Welsh crosses also started life heavier than the Blackface but by weaning were about 6% below and remained thus.

For the other crosses, shown in Figures 2c and 2d, there was a general tendency from weaning onward for crosses with the Southdown to exceed in



2a



2b 2c 2d

FIG. 2. Breed deviations in body weight, from Blackface, expressed as proportions of the fitted base (%) (base class defined in Fig. 1); (*a*) from birth to 5½ years, (*b*), (*c*) and (*d*) from birth to 1½ years. (*a*) Scottish Blackface (B), Cheviot (C) and Welsh Mountain (W) and their crosses. B ——; C – – –; W·····; BC — | — | —; BW — · — · —; CW —△—△—. (*b*) Crosses of Lincoln Longwool (L) and B, C and W breeds with Lincoln. B ——; BL – – –; CL — · — · —; WL .....; L — | — | —. (*c*) Crosses of B, C and W breeds with Tasmanian Merino (M). B ——; BM – – –; CM — · — · —; WM ·····. (*d*) Southdown (S) (not adjusted to Blackface dam) and crosses of B, C, and W breeds with Southdown. B ——; BS – – –; CS — · — · —; WS ·····; S — | — | —

weight those with the Merino, and Cheviot crosses to exceed Blackface crosses. The weights of the Southdowns which are confounded with the Southdown maternal effect are akin to those of the Welsh breed except prior to weaning when they were notably lighter in weight.

In respect of body weight there was some evidence of differences among breeds and crosses (hereafter generally referred to jointly as 'breeds'—in inverted commas) in rate of maturity. Strictly, data from the BCW analysis alone are useful for this purpose since only for them is a reasonable estimate of mature body weight available. The results showed the Cheviot to be the fastest maturing by a small margin with the Blackface-Cheviot cross the slowest. For the remaining 'breeds' there was considerable overlap and the greatest difference at any age between the extremes was only 7%.

For the 'all breeds' analysis, data stopped when the animals were 75 weeks old. The BCW analysis had suggested that at this age there were still appreciable 'breed' differences in the stage of maturity of body weight (varying between 79% and 86%). Hence accurate estimates of mature weight could not be made for the Lincoln, Merino and Southdown breeds and crosses and an analysis of differences in their rate of maturing did not seem meaningful.

Linear dimensions. Data similar to those presented in Figure 2 for body weight were also available for the six linear measures of body size taken at 6-weekly intervals from 6 weeks to 222 weeks for the BCW group and to 72 weeks for the other 'breeds'. However, these will not be discussed in detail here. Instead these data have been used to consider the following question: is there 'breed' variation in the six linear dimensions which is independent of body weight? For example, is a Welsh sheep simply a proportionally smaller version of a Lincoln or is it taller, longer, wider, etc?

In an attempt to answer this question, the fitted values, obtained for each pure breed and cross at each age by the original least squares analysis, were used as the basic data for a further analysis. To remove variation in the weights and linear dimensions due to seasonal and random fluctuations, average values were calculated for the following ages: 30–48, 54–72, 78–96, 102–120, 126–144, 150–168, 174–192 and 198–222 weeks. Since rapid changes occurred during the first 30 weeks the ages 6, 12, 18 and 24 weeks were considered individually. This procedure gave a set of 12 weights and measurements for each of the 'breeds' in the BCW analysis and a set of six for each of the other 'breeds'. Consideration of the ratios of linear dimensions to body weight showed that within each 'breed' this ratio always declined with age, this decline being initially rapid and slowing down as the animals approached maturity. It was also apparent that the lighter 'breeds' had, at all ages, a higher dimension:weight ratio than the heavier 'breeds'. This suggested that there was an underlying physical relationship between body weight and linear dimension of the form:

$$\frac{\mathrm{LD}}{\mathrm{Wt}^b} = K$$

where LD = linear dimension, Wt = body weight, b = a constant for any given linear body dimension and K = a 'breed' constant for any given linear dimension.

Taking natural logarithms of this equation gives a regression equation of the form:

$$\text{Log (LD)} = \log K + b \log (\text{Wt})$$

This regression was fitted by a least squares analysis using the data obtained from previous analyses for the age classes described above. It was found that for all the linear dimensions except body length there was no significant 'breed' variation in the slopes (b). Moreover, slopes based on the first six age classes did not differ significantly from those based on all 12 except for tibia

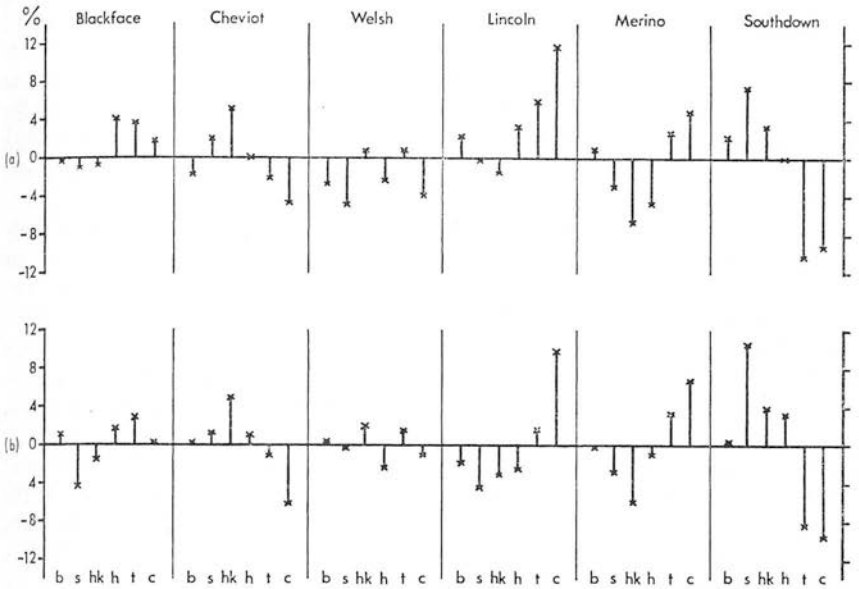


FIG. 3. (*a*) Relative body conformation of six breeds independent of body weight expressed as deviations of K values from average as a proportion of their average (%) (for definition of K see text). (Deviations (%) have an approximate SE of 2·5). (*b*) Relative body conformation when linear body dimensions were close to their mature size (see text). (Deviations (%) have an approximate SE of 5·0). b = body length; s = shoulder width; hk = hook width; h = head width; t = tibia length; c = cannon length.

length. The analyses provided estimates of b and of log K for the 'breeds' for each of the six linear dimensions. The values of K differed significantly among the 17 breeds and crosses for which they were calculated. This suggests that when considered independent of weight there was significant 'breed' variation in the shape of the animals. The 'breed' variation in the regression, b, for body length also suggests differences in shape.

In order to compare the dimensions of the pure breeds involved, including the Merino, which only occurred in crosses, the mean breed K values when each sire breed was mated with Blackface, Cheviot and Welsh females were determined. The values so obtained were doubled in order to estimate the potential differences attributable to the pure breeds. Figure 3a shows the deviations (as percentages) of the six pure breeds from their average for the value of K for each dimension. For body length where each K value was calculated using a separate b value for each breed the deviations apply at

50 kg live weight, close to the flock average at 54 to 72 weeks of age. As seen from Figure 3a Cheviots and Southdowns were relatively wide at shoulder and hooks and short in the leg whilst the Lincoln was particularly long in the leg and the Merino narrow in body.

The six linear body dimensions differed in their rate of maturity. This was apparent from inspection of the growth curves of each part, and from consideration of the regressions (*b*) of linear dimension on weight calculated as described earlier. For the animals in the BCW analysis where observations continued to $4\frac{1}{4}$ years of age the pooled regressions (based on average values for the 12 age classes as before) were in order of magnitude: hook width 0·45, body length 0·30, shoulder width 0·27, head width 0·21, tibia length 0·20, and cannon bone length 0·17. Particular reservations apply to the value for body length since values differed significantly among the breeds and crosses, and to that for tibia length where the slope was significantly steeper in the earlier than the later part of the period. However, it appears that dimensions which mature quickly have low *b* values while those which mature more slowly have higher *b* values.

The comparison in Figure 3a is among breeds separately for each body dimension. It is possible, however, that differences in the stage of maturity of each body part reached by different breeds at a given weight may have contributed to the differences shown. A further indication of breed differences was sought, therefore, for linear dimensions at, or close to, their mature size (in the period 54 to 72 weeks for all breeds) but, on this occasion, by comparing the dimensions of body parts relative to each other within breeds. For each body part the average size of each breed or cross was expressed as a percentage deviation from the mean of all breeds and crosses; estimates were then obtained, as before, for each of the six pure breeds involved. On this basis some, like the Lincoln, were clearly above average for all parts whilst a breed like the Welsh was consistently below. In order to standardize the comparisons of shape among the breeds, the deviation of each body part was expressed as a difference from the percentage deviation averaged over all linear body parts for each breed (e.g. the cannon bone length deviation of the Lincoln exceeded the average percentage deviation of all body parts of the Lincoln by 9·9%—see Fig. 3b). The results provide a crude breed comparison of shape at mature size. This is illustrated in Figure 3b. Shape is seen to differ among breeds mainly in respect of the relationship of body width to leg length, but Welsh were more of an 'average' shape at maturity, while Lincoln were relatively narrower in body not just longer in leg and in this respect of similar conformation to the Merino.

Effects of individual sires

The individual rams, used as fathers of the present sheep, within each breed and each year, contributed significantly ($P<0{\cdot}05$) to variation in body weight and all linear dimensions, except tibia length, at most times throughout life. However, differences between the two sires within any breed in any one year, as judged by their daughters, were rarely large. There were some exceptions, for example one pair of Welsh rams had daughters which differed by up to 12% in weight from each other. The majority of such differences were less than 5%, not often statistically significant and not always consistent in direction. There were rather more significant differences between pairs of

sires for body length and cannon bone length at relatively mature ages than the isolated cases noted for the other dimensions or for body weight.

Heterosis

Estimates of heterosis were obtained by comparing the crossbred animals with the average for the contemporary parental pure breeds. As this is only meaningful when the maternal effect has been removed from the breed effect, the estimation could only be done for the crosses of the Blackface, Cheviot, Welsh and Lincoln breeds. Heterosis was estimated for each of the possible crosses in respect of body weight and the linear dimensions at each age. The deviations are shown in Table 2 as proportions of mid-parental values for a selection of ages. This takes into account the initial period of rapid growth and thereafter a summer and a winter observation to allow for the possibility that the expression of heterosis varies with season and hence the condition of the animal. Table 2 shows that there was no consistent crossbred superiority in any of these traits for the Blackface-Welsh or Cheviot-Welsh crosses, at any age. For the Blackface-Cheviot cross, however, there was evidence of crossbred superiority in body weight, body length, shoulder width and hook width but this did not appear until around 72 weeks of age. Data for the crosses with Lincoln were only available up to 72 weeks of age. For these there was evidence of heterosis in body weight, emerging from about 6 months of age and increasing thereafter. There was also some evidence of heterosis appearing in several body parts particularly in the Blackface-Lincoln cross.

Since a considerable proportion of the deviations of the Cheviot-Welsh cross from midparent values were negative, including a few significant deviations, there is at least a suggestion that these crosses may be a little smaller than expected.

Maternal effect

Maternal environment significantly affected the size of lambs at birth and up to 12 weeks of age for the linear measures and for the first year of life for weight. Results are shown in Table 3 only for this early period and are presented as deviations from the Blackface breed for a selection of ages. At birth, lambs born to Lincoln mothers were 14% heavier, but this advantage rapidly diminished and remained at about 5 to 6% above Blackface for the next 18 months. The smaller deviations of lambs born to Cheviot and Welsh mothers disappeared after about 1 year.

Sex

Male lambs were only recorded from birth to weaning. Deviations of male from female (BCW analysis) are shown in Table 4. Corresponding figures from the 'all breeds' analysis were virtually the same for the linear body dimensions, but for body weight males deviated by about 1·2% less from females than the figures shown in Table 4. Males were heavier and generally larger than females. The deviation for body weight increased with age quite markedly.

Birth type and rearing

Birth type and rearing had its most marked effect in the first 6 months of the lamb's life as seen in Figure 4. Twins reared as singles (t/s) up to weaning had almost reached the weight of single-born lambs (s/s) by 9 months of age

TABLE 2

The difference between the crossbred and the mean of the parental breeds (cross-pure) as proportions (%) of the mean purebred value for body weight and the six linear dimensions

Cross	Age† (weeks)	Body weight	Body length	Shoulder width	Hook width	Head width	Tibia length	Cannon length
B × C	6	−0·6	0·1	−1·2	−1·4	0·2	0·3	−0·7
	18	2·9	1·0	−1·2	−1·3	0·4	0·6	0·2
	42	1·2	2·3*	3·7	2·2	1·5*	0·4	0·3
	72	3·9*	1·9*	2·0	0·7	1·3	1·6	1·0
	90	3·6	3·2**	8·5**	5·0**	1·6	4·4**	3·7**
	120	3·4	2·9**	−2·0	−1·9	1·9**	0·1	1·5
	144	5·3*	2·9**	14·6**	5·6**	1·1	−0·1	0·5
	174	7·4**	2·6**	−3·7*	−2·7*	2·6**	0·8	1·7
	198	8·8**	2·9**	13·2**	4·5**	1·5*	−0·8	−1·0
	222	9·4**	3·2**	20·9**	9·2**	0·8	−0·0	2·0
B × W	6	1·4	0·3	−0·7	0·2	0·7	0·5	0·0
	18	0·2	0·7	2·4	1·3	0·7	−1·4	0·3
	42	−0·9	1·1	−3·0	−3·2	1·1	−1·0	−1·9
	72	1·2	0·5	1·5	0·4	0·9	−0·6	0·1
	90	1·2	0·9	−1·1	−1·4	1·3	0·1	0·5
	120	1·6	0·0	3·5*	2·8*	1·1	−0·9	−0·8
	144	2·8	0·9	5·5*	1·9	0·7	−0·3	−0·8
	174	1·9	0·1	1·2	1·4*	0·7	−1·0	−0·5*
	198	1·1	−0·2	4·7*	0·9	0·2	−2·5*	−0·5
	222	1·5	0·5	3·7	3·7*	0·5	−0·9	0·0
C × W	6	0·6	0·6	−0·2	−0·2	0·5	0·8	0·8
	18	−1·7	−0·5	2·0	−1·0	−0·8	−1·5	1·7
	42	−2·3	−0·8	−2·0	−3·0	−0·6	−0·2	0·2
	72	−1·5	−0·5	−0·6	−0·2	−0·5	−0·5	1·1
	90	−2·1	−1·6	−7·8**	−4·4**	0·4	0·6	1·5
	120	−3·3	−0·7	2·8	0·3	−0·5	0·2	1·0
	144	−2·9	−1·5	−5·8*	−2·4	−0·0	0·5	1·7
	174	−1·8	−0·3	4·0*	2·2	−0·0	−0·7	0·6
	198	−1·7	−1·7	−2·7	−1·8	−0·3	−1·6	2·2
	222	−3·4	−2·4**	−7·2**	−4·8**	0·3	0·7	0·2
B × L	6	−1·0	−1·9	−3·0	−2·2	1·7	0·4	−1·1
	18	9·0	1·5	0·6	−0·1	4·7**	0·7	2·5
	42	10·1*	4·8*	3·1	2·8	5·3**	6·7**	2·4
	72	9·5**	4·6**	−1·6	2·5	4·1**	4·1*	2·2
C × L	6	−4·1	−3·4*	−1·8	−2·9	0·6	−1·9	−0·7
	18	2·4	−2·8	−3·5	−3·0	−0·2	0·2	−1·4
	42	4·4	−1·1	−3·1	−4·5	1·6	5·8*	2·2
	72	6·8	1·5	3·9	1·9	2·0	2·3	−0·1
W × L	6	1·4	0·0	0·1	−0·1	0·4	−0·7	0·3
	18	4·3	0·9	0·7	2·6	0·2	1·2	0·6
	42	5·2	0·6	−8·4**	−4·8*	−0·8	1·7	−1·1
	72	8·0**	3·1**	5·9**	3·6*	1·2	0·3	−0·5

* Deviation significant at 5% level. ** Deviation significant at 1% level.

† Observations at weeks 42, 90, 144 and 198 fell in mid-winter (January–February), those at 18, 72, 120, 174 and 222 in summer (July–August) and '6 weeks' fell in May.

TABLE 3

Maternal breed deviations from Blackface (as proportions (%) of the fitted base) for six linear body dimensions†

Dimension	Age (weeks)	Maternal Breed			Significance of variation
		Cheviot	Welsh	Lincoln	
Body weight	birth	−4·6	−9·8	17·9	**
	6	−3·7	−7·8	5·0	**
	12	−4·9	−7·4	6·7	**
	18	−6·9	−2·9	6·7	*
	42	−6·5	−2·5	5·5	NS
	72	−2·0	1·2	4·6	NS
Body length	6	1·6	−2·5	1·7	**
	12	0·5	−1·0	3·0	*
Shoulder width	6	−3·0	−3·7	2·1	**
	12	−2·7	−1·9	7·2	**
Hook width	6	−0·6	−3·5	1·8	**
	12	−2·5	−2·3	6·8	**
Head width	6	0·2	−0·7	3·8	**
	12	0·0	0·1	3·8	*
Tibia length	6	−2·0	−2·6	3·6	**
	12	0·5	−2·0	1·3	**
Cannon length	birth	−0·2	−3·4	3·0	**
	6	1·2	−1·5	3·1	**
	12	1·8	0·0	3·4	**

* Variation significant at 5% level. ** Variation significant at 1% level.
NS non significant.
† From the age of 18 weeks onward the deviations were not significant, except for weight.

TABLE 4

Deviations of male from female (as proportions (%) of the fitted values for female)

Age (weeks)	Body weight	Body length	Shoulder width	Hook width	Head width	Tibia length	Cannon length
0	5·6**	—	—	—	—	—	2·4*
3	4·6**	—	—	—	—	—	—
6	5·7**	0·7NS	1·2NS	−0·3NS	4·9**	3·9**	4·0**
9	7·4**	—	—	—	—	—	—
12	8·2**	2·1**	4·1**	1·7*	5·4**	2·5**	3·5**
15	9·1**	—	—	—	—	—	—

* Deviation significant at 5% level. ** Deviation significant at 1% level.

but twins reared as twins (t/t) did not come to within 5% of the weight of singles until almost 18 months old. However, even during their last year of life (4·5 to 5·5 years) twins reared as twins were on average about 3% lighter than single-born animals reared as singles, and triplets which were reared as

twins up to weaning (tr/t) were still about 5% lighter. Variation attributable to the combined effects of birth type and rearing was statistically significant up to 3 years old.

All linear dimensions were significantly affected by birth type and rearing early in life and up to 12 weeks old the order of size was, as expected, s/s>t/s>t/t>tr/t. As for body weight, the twin-reared groups never quite reached the size of the single-born and single-reared sheep in respect of body

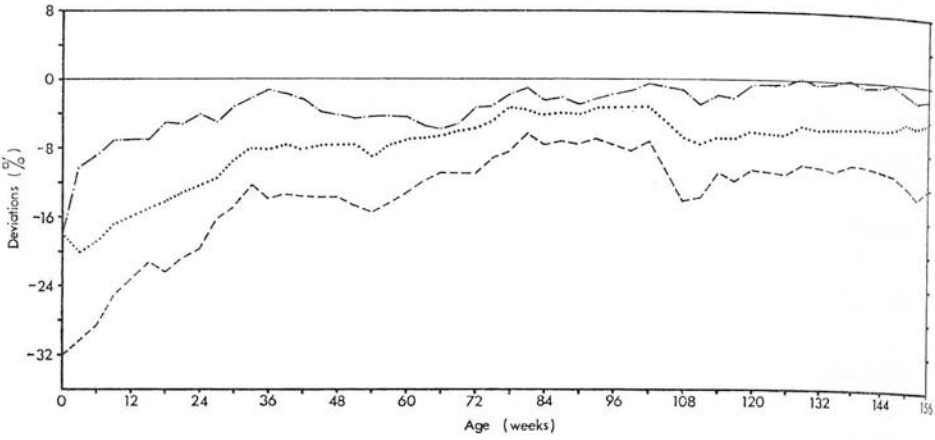


FIG. 4. Effects on body weight from birth to 3 years of birth type and rearing shown as deviations from single-born lambs reared as singles and expressed as proportions of the fitted base (%). s/s ——; t/s —·—·—; t/t ·····; tr/t – – – –.

length, shoulder width, hook width and head width but for tibia length and cannon bone length they had caught up by about 72 and 54 weeks old respectively. Variation attributable to the effects of birth type and rearing was statistically significant ($P<0{\cdot}05$) up to about weaning for leg length, and at least to a year old for the other dimensions.

Week of birth

All animals were grouped according to their week of birth. This factor was only consistently a significant source of variation for body weight and linear dimensions prior to weaning. In general animals born early or late in the season were lighter and smaller than those born in between. However, all differences were small.

Age of dam

All dams were born in 1955 and lambed in 1957, 1958 and 1959 (BCW animals only), so that age of dam was completely confounded with year of birth. Also, different pairs of rams within each breed were used each year so that there was further confounding with sire-pair effects.

Between birth and 18 weeks the difference in weight between lambs born to ewes of 2 and 3 years old, in 1957 and 1958 respectively, was small and generally non-significant, while lambs born in 1959 to 4-year-old ewes were generally significantly heavier up to 18 weeks old. Differences in body

weight attributable to the year in which the animals were born (and the age of their dam) re-emerged as large and significant effects around each successive period of parturition. These differences, however, varied in sign suggesting that the differences cannot be simply attributed to year of birth (age of their dam) but that the results are also affected by conditions associated with the year of parturition.

For the 6 linear body dimensions, the combined effects of age of dam and year were significant at most times throughout life but there was no particular pattern.

Correlations

Table 5 gives the mean residual correlations (within age, averaged over all ages from 6 weeks to 222 weeks) among the various measures of size together

TABLE 5

Residual correlations between the measurements, from the BCW analysis. Means and ranges are calculated for each correlation over all ages

	1 Body weight	2 Body length	3 Shoulder width	4 Hook width	5 Head width	6 Tibia length	7 Cannon length
1 Mean	1						
Range	—						
2 Mean	0·65	1					
Range	0·47–0·78	—					
3 Mean	0·58	0·45	1				
Range	0·36–0·74	0·22–0·69	—				
4 Mean	0·60	0·48	0·71	1			
Range	0·42–0·75	0·30–0·70	0·50–0·85	—			
5 Mean	0·45	0·41	0·24	0·27	1		
Range	0·28–0·62	0·29–0·61	−0·14–0·61	0·00–0·58	—		
6 Mean	0·40	0·40	0·09	0·16	0·39	1	
Range	0·23–0·61	0·19–0·57	−0·34–0·41	−0·20–0·45	0·23–0·54	—	
7 Mean	0·39	0·40	0·10	0·17	0·37	0·59	1
Range	0·30–0·49	0·17–0·55	−0·24–0·32	−0·15–0·36	0·24–0·51	0·37–0·70	—

with the range of values found. High correlations existed for weight with body length, shoulder width, and hook width, for shoulder with hook width, and for tibia with cannon bone length. There appeared to be no trends associated with age or season.

Low and generally non-significant correlations were found for shoulder width with head width, tibia length and cannon bone length, and for hook width with tibia length and cannon bone length. For the first two of these correlations there was some indication of a decrease with age.

The remaining correlations were moderate and, in general, statistically significant. Correlations showing a marked decrease as the animals grew

older were: body weight with head width, tibia length and cannon bone length; body length with shoulder, hook and head width, and hook with head width.

Correlations between successive body weights were generally high, in the region of 0·9 except around lambing when these correlations were between 0·5 and 0·7. Correlations between successive measurements of the same linear dimension were generally lower and more variable than for weight possibly because of errors in measuring the animals. Such correlations averaged around 0·8 for cannon bone length and head width, 0·7 for body length, 0·6 for hook width and tibia length and 0·5 for shoulder width.

Residual correlations between the animal's body weight from birth to 2 years and the weight of its dam at 21 months old were also calculated. These were low, around 0·15 in the early weeks but rose to 0·28 by 2 years of age.

DISCUSSION

The breeds and crosses in the present study differed quite markedly from each other in body weight and in linear body dimensions. In general, the pure breeds involved ranked in the same order, with respect to body weight, as did their mothers studied by Wiener (1967). This agreement in ranking was particularly close when allowance was made for the combined contributions of breed and maternal effect. For example, in the pure breeds the slight early breed advantage in weight of the Cheviot over the Blackface was more than wiped out by the advantage of the Blackface maternal environment over that provided by the Cheviot.

In the present study the range of breed values was reduced; this may be in part a consequence of the adjustment of the figures (except for Southdown) to a constant maternal (Blackface) environment. However, even when only the purebred values of the breeds, unadjusted for maternal effect, were considered, the variation in weight among breeds was less. For example, the Lincolns were lighter and the Welsh markedly heavier than in the former study. Therefore effects of the differing early farm environments for the different breeds in the previous study must also have affected the comparisons.

Breed differences were demonstrated in conformation. Thus, Welsh Mountain sheep (the lightest in weight of the common British breeds) were not simply a proportionally smaller version of Lincoln Longwool (one of the heaviest of breeds) or Scottish Blackface.

It is apparent from the results that heterosis for body weight, though found for some crosses, may be entirely absent for others. Heterosis may first appear at quite different stages in life and even when present may show marked differences in magnitude in different breed combinations and with time. This is perhaps not entirely surprising in view of the conflicting reports on heterosis in the literature. For example, Donald, Read and Russell (1963) found heterosis in the Swaledale-Scottish Blackface cross to be only around 3% at birth rising to about 5% at 3½ years, while Ghoneim, Aboul-Naga and Labban (1968) found heterosis in the Ossimi-Merino cross to be around 10% at birth rising to about 40% at 1½ years. It is possible in some cases that crossbreds can appear to be superior if one of the pure breeds is unable to realize its full potential. For example, it may be argued for the present results that the Welsh-Lincoln cross exceeded the mid-parent value only because the environmental conditions did not allow the pure Lincoln to grow

to its full size. However, in this instance the answer is clearly not so simple since the crosses of Lincoln with Blackface and Cheviot were heavier than the pure Lincoln from 18 weeks of age onward. It is not known whether a different environment might have produced different results since the role of genotype-environment interaction in the observed manifestation of heterosis has not been examined.

Because maternal effects could not be separated from breed effects for the pure Southdown similar estimates of heterosis could not be made for the Southdown crosses. However, the results suggest that hybrid vigour may well have contributed to the weights of these crosses since they approached or exceeded the weights of what is likely to have been the heavier parental pure breed contributing to each cross.

Heterosis in linear body dimensions was also found for some crosses and not others. Body length, shoulder width and hook width behaved in a similar fashion to body weight (except for the Cheviot-Lincoln cross), but head width showed heterosis only for crosses of Blackface with Cheviot and Lincoln. For the two measures of leg length indications of significant heterosis were even more isolated and the effects when present were small.

These results show clearly that any general statement regarding the importance of heterosis in growth is inappropriate, and that much depends upon the breeds involved and the precise measure of growth.

In so far as the degree of heterosis manifested by a cross may indicate the degree of genetic similarity of the parent breeds involved, it is of interest to note that the most general indications of heterosis for body weight in the present study arose in crosses of the Lincoln and probably the Southdown with the three hill breeds (Fig. 2). It seems reasonable to suppose that breeding aims differed in the respective development of the lowland and the hill breeds leading to a differentiation in gene frequencies. It is also of interest to note that among the three hill breeds the only cross to show some heterosis (the Blackface-Cheviot) was that which Rasmusen, Hall, Hayter and Wiener (1974) found in later generations of this flock to differ quite markedly in frequencies at several blood group loci. The other two pairs of hill breeds did not differ in this way, nor when crossed, showed any heterosis in any aspect of body size.

Whilst in a pure breeding situation which applies in, for example, most hill flocks in Great Britain, breed effects are confounded with maternal effects, the design of the present experiment has enabled the separation of maternal effect from breed effects, in most cases at least. Information of this type provides an opportunity to combine breeds in a crossbreeding system to gain maximum advantage. The results show that maternal performance is partly independent of maternal size. For example, in relation to their own mature weight, the Welsh dams can be seen to have provided the best environment for their lambs as judged by birth weight. At the other end of the size scale the Lincoln produced the lightest lambs at birth when related to the high mature weight of the Lincoln dam. Studies involving egg transfer have looked particularly critically at combinations of different breeds of lamb and dam with widely differing body weights (Hunter, 1956; Dickinson, Hancock, Hovell, Taylor and Wiener, 1962; and Bradford, Taylor, Quirke and Hart, 1974). These studies revealed that a small breed of lamb from a large breed of dam does not benefit, in terms of birth weight, to the same extent as the corresponding restriction imposed on a large breed of lamb in

a small breed of dam. In the present study Lincoln ewes were crossed to a breed smaller than themselves and Welsh ewes to breeds larger than themselves. This may have affected the expression of maternal breed differences in birth weight if the cross with Lincoln ewes did not fully utilize the resources of the large dam breed, while the crosses to Welsh ewes may have used the resources almost to the small dam breed's full capacity. The relative merits of different breeds as mothers of lambs must, therefore, depend heavily on the precise breed combinations.

The breeds involved here also differed in post-natal maternal effect. In relation to their own mature weight, or their mature metabolic weight ($Wt^{0.73}$), the advantage of the Welsh relative to the Blackface became greater as reflected by the growth of their lambs between birth and weaning, while the relative disadvantage of the Lincoln became more pronounced and the Cheviot remained more or less the same.

Maternal effects were significant for body weight of the lamb only until about 1 year of age and for the linear dimension only until weaning. Although there have been a number of published studies of maternal effects few have examined these beyond weaning. The transient nature of the maternal breed effects found in the present experiment has, however, also been noted by Karihaloo and Combs (1971) for weight and cannon bone length.

The effects of birth type and type of rearing are similar to maternal effects in being particularly important early in the life of the lamb. Effects of birth type on birth weight and of birth type and rearing on weaning weight have been quite extensively studied (for example, Bichard and Cooper, 1966; Sidwell and Miller, 1971) and the differences found here fall within the range reported by others. However, the effects were seen in this study to persist for the later-maturing body parts, and especially for weight, for several years of the animal's life. Terrill, Sidwell and Hazel (1948) and Karam (1959) who recorded size at 1 year of age found differences of 3 to 5% between singles and twins.

Parity effects, which would normally call for consideration along with the other environmental influences on lamb size, could not be independently assessed in the present study.

The residual correlations between body weight and the linear dimensions and among the dimensions themselves, show that there is a marked degree of independence in the size of the separate parts. A similar conclusion might be drawn from the simple correlation coefficients among measurements at birth and among others at weaning published by Galal, Cartwright and Shelton (1965) on 1400 lambs of a variety of breeds. The coefficients ranged from 0·07 to 0·85. The correlations in Table 5, equivalent to correlations within sub-classes, underline the point made from a consideration of the different breeds and crosses, that the animals are not scale versions of each other with size depending solely on body weight.

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MATERNAL PERFORMANCE IN SHEEP AS AFFECTED BY BREED, CROSSBREEDING AND OTHER FACTORS

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SUMMARY

Maternal performance of female sheep of three hill breeds, Scottish Blackface, Cheviot and Welsh Mountain, and the crosses among these breeds has been studied in terms of lifetime production and some of its components. The data are based on 193 ewes, which were given the opportunity of having four annual lamb crops, and their lambs.

There was no significant variation among the breeds and crosses in ewe survival or in the proportion of barren ewes at each lambing.

There was significant variation among the breeds and crosses in the number of lambs born per ewe lambing, in lamb survival and in weights of lamb at birth and at weaning. Crossbred ewes (producing crossbred lambs) had more and heavier lambs than expected from the average of the pure breeds contributing to each cross, but the three crossbred types differed in the amount of heterosis shown. Over their lifetime in the flock there were significant breed differences in the total weight of lambs weaned, with crossbred ewes producing about 9% more than the average of the parent breeds involved. The crossbred ewes produced more weight of lambs over their lifetime than pure Cheviot or pure Welsh Mountain ewes, but not as much as pure Scottish Blackface.

Effects of parity of dam and of sex, birth type, and type of rearing of lamb are given.

INTRODUCTION

CROSSBREEDING is widely practised with hill breeds in Great Britain to produce sheep for use on lower ground. In the hills themselves, however, the different breeds of sheep are traditionally kept in different areas or at least on different farms. There is relatively little information, experimental or practical, on whether breed substitution or crossbreeding might offer advantages. Among the few studies in Great Britain, apart from the present experiment, are those by the Hill Farming Research Organisation (e.g. Gunn, 1967) comparing North with South Country Cheviots and Scottish Blackface, and Donald, Read and Russell (1963) comparing Swaledale with Scottish Blackface and their crosses.

The present paper deals with reproductive and postnatal maternal performance of three hill breeds common to Great Britain and of the crossbred females produced from among these breeds. The breeds involved are the Scottish Blackface, the Cheviot and the Welsh Mountain but the com-

parisons were made on an upland, grassland farm not on a traditional hill farm. Performance was assessed in terms of lifetime production and its component traits. The growth of these sheep was previously examined by Wiener and Hayter (1974) and the performance of their dams by Wiener (1967).

The study reported here is one stage of a long-term experiment involving purebreeding, crossbreeding, inbreeding and the crossing of inbred lines. The sheep studied in this paper were mated to produce both non-inbred and inbred progeny and the paper incorporates the results of both sets, although it is not the intention to discuss the effect of inbreeding of the lambs in any detail in this paper except in so far as it affects the maternal performance of their dams.

MATERIAL AND METHODS

Animals and observations

The sheep comprised three breeds, the Scottish Blackface ('Blackface'), the Cheviot (South Country type) and the Welsh Mountain ('Welsh') and first crosses (F_1) among them (all referred to hereafter as 'breeds'). The 'breeds' were run as one flock, at grass, on the upland farm (elevation approx. 300 m) of Blythbank, Peeblesshire, Scotland, where they were born over a 3-year period to females bought as lambs for a long-term experiment involving crossbreeding and inbreeding. Particulars of the foundation population and the flock management were given by Wiener (1967) and further information relevant to the sheep in the present study by Wiener and Hayter (1974) who studied body size from birth to maturity. The female sheep surviving to reproductive age are now examined in respect of their reproductive and postnatal maternal performance.

The females were first put to the ram at approximately 19 to 20 months old and annually thereafter for up to 4 years. A mating was observed to take place for each surviving sheep put to the ram each year except for two females which did not come on heat in two successive years and were culled thereafter and found to be hermaphrodite. However, these two ewes have been included in the mating records. No other culling occurred. Lambing started at the beginning of April each year.

In the first year of mating each female was put to a contemporary but unrelated male (ram) of the same breed or cross from the same flock, to produce a non-inbred generation of progeny (F_2 in the case of crosses). In the second year approximately half the females were mated to their own sons born that year to produce (25 %) inbred progeny, the other half again to the unrelated rams used previously. In the third year this scheme was repeated except that the proportion of mother × son matings was higher because rams born in two years were available. In the fourth year only unrelated rams used previously were again put to the females (ewes). Statistical allowance has had to be made, as described later, for possible differences arising in the reproductive and maternal performance of ewes as a consequence of the two classes of matings (in the second and third year). To avoid confusion with other nomenclature the class of ram used in any mating (i.e. the class of sire of the lamb) will be referred to as the 'phase' (of mate or of sire), and will be denoted O_1 (equivalent to F_1 in the crossbreds) for rams unrelated to the ewe (but of the same breed or cross) or O_2 (equivalent

to F_2 in the crossbreds) for rams related to the ewe (mother × son mating). Thus, an O_1 ram produced an outbred lamb (F_2 in the crossbreds) and an O_2 ram an inbred (25%) lamb.

Ewes with single or twin lambs were generally expected to rear these unaided. Ewes with surviving triplets (there were no larger litters) had at least one lamb removed. Whenever possible, triplet lambs, any lambs whose mothers had died and a very small number of twin lambs neglected by their dams were fostered as singles by ewes which had lost their own lambs. No account was taken of 'breed' in the fostering process. Thus, some 'breeds' fostered more lambs than were removed from them, while the reverse was the case for others. A total of 31 of the 1152 lambs born were fostered, but it affected 50 of the 705 lambing records. A few lambs also had to be reared artificially.

Records were kept of mating and lambing dates, number of lambs born,

TABLE 1

Number of ewes and lambs by 'breed' and phase of mate of ewe (sire of lamb)

	Phase of mate (or of sire)	'Breed' groups							
		Blackface (B)	Cheviot (C)	Welsh (W)	B × C	B × W	C × W	Total number	
ewes starting		21	23	26	42	45	36	193	
ewes finishing		18	16	21	31	41	29	156	
of mating records	O_1	56	57	69	100	121	95	498	705
	O_2	24	22	27	44	53	37	207	
of lambing records	O_1	55	54	67	96	117	90	479	679
	O_2	23	19	27	42	52	37	200	
of lambs born	O_1	101	85	102	173	182	143	786	1152
	O_2	41	29	43	74	113	66	366	
of lambs weaned	O_1	88	67	95	149	171	130	700	1003
	O_2	25	24	33	57	108	56	303	

lamb and ewe mortality, lamb weights at birth and weaning (15 weeks old), and ewe weights in January of each year, and of the type of rearing (natural, fostered, etc.).

Statistical procedure

Analyses were performed on five sets of data, three of which pertained to the 193 ewes involved and the others to the 1152 lambs born to them. Numbers are shown in Table 1. The analyses took the form of fitting a linear model by the method of least squares with parameters representing the effects of: breed or cross of animal, year of birth of lambs, parity or age of ewe, phase of mate or sire (O_1 or O_2), sex of lamb, birth type and rearing of lamb, week of birth of lamb and individual sire of the ewe. Interactions between 'breed' and phase of mate (or sire) and between breed of sire of ewe and year of birth of ewe were also fitted. The exact model used varied according to the set of data used; for example, sex and birth type and rearing

were appropriate only for analyses of data pertaining to lambs. The effect of individual sire of ewe and the interaction terms were statistically significant only for some traits considered, but were retained throughout for consistency. For the analysis on lifetime production of 193 ewes it was not appropriate to fit directly for phase of mate since the way inbreeding was carried out meant that the ewe's prolificacy at the first lambing influenced the probability that she would be able to be mated to her son on the next occasion. To avoid this problem, results from the analysis of the 705 mating record were used to adjust the lifetime performance records, within 'breed', to a non-inbred level.

RESULTS

Results are presented in relation to the Blackface breed with year effects averaged. For ewes the results were adjusted to first parity (except for lifetime production) and to O_1 matings. The base class for lambs was adjusted to non-inbred females born and reared as singles and with 2-year-old dams. Since the results for the effects of 'breed' derived from mating ewes to O_1 or O_2 rams differ markedly for some traits, both sets are presented wherever appropriate.

Effect of 'breed' and heterosis

Number of mating records. This relates to females which had reached the prescribed age at first mating and is a measure of ewe survival. Females present at the start of the study had, on average, 3·79 mating records when expressed in terms of the Blackface base class (unadjusted flock mean 3·64). Females surviving to the maximum of four matings numbered 156. The first column of Table 2 shows that neither the variation among the 'breeds' nor the individual 'breed' deviations from the base class were significant. Crosses did not differ significantly from the pure breeds.

Proportion lambing. The proportion of ewes lambing from among those mated indicates the effect of barrenness, however caused, on ewe and flock performance. Table 2 shows that it did not vary significantly among the 'breeds'. Crossbreds were trivially poorer than expected on the basis of mid-parental values when mated to unrelated (O_1) rams and very slightly better in matings to related (O_2) rams. However, the 'breed' × phase interaction was not significant. When ewes were mated to their sons the proportion lambing declined on average by 3% and although this difference from matings to unrelated rams was not significant, it suggests that barrenness at the time of lambing was not solely attributable to the ewe.

Litter size. As shown in Table 2 'breeds' differed significantly in litter size at birth irrespective of phase of lamb but the relationship of crossbreds with purebreds was altered. On average, crossbreds were at a greater advantage relative to the purebreds when inbred lambs were born. The 'breed' × phase interaction was significant ($P < 0{\cdot}05$). On average, litter size was reduced by 0·16 lambs when ewes were mated to their sons to produce inbred lambs compared with a mating to an unrelated ram.

Lamb survival. 'Breed' variation was significant within each phase (Table 2). More lambs from crossbred ewes survived than from purebred ewes, but, as for the other traits, the crossbred advantage was more marked when judged on inbred lambs than on non-inbred lambs. The 'breed' × phase interaction was significant ($P < 0{\cdot}01$), with the Blackface and Welsh showing

markedly better survival when judged on their outbred lambs. In general, inbred lambs survived less well (the proportion being on average 0·08 less) than non-inbred lambs.

Weight of lamb. Table 3 shows birth and weaning weights for lambs, adjusted to the weight of single-born and, in the case of weaning weight, single-reared female lambs. At birth the Cheviots were heaviest among the pure breeds and Welsh the lightest. Crossbreds were slightly heavier than

TABLE 2

Effect of breed and crossbreeding and of phase (of mate or sire) on lambing performance of ewes and on lamb survival to weaning

	No. mating records per ewe at start	Proportion lambing per ♀ mated		No. lambs born per ♀ lambing		Proportion lambs surviving per lamb born	
		O_1 mate	O_2 mate	O_1 mate	O_2 mate	O_1 sire	O_2 sire
of records	193	498	207	479	200	786	366
of							
ackface (B)	3·8	0·97	0·92	1·70	1·47	0·82	0·55
eviot (C)	3·5	0·94	0·83	1·45	1·22	0·75	0·79
lsh (W)	3·7	0·96	0·95	1·37	1·22	0·89	0·74
C	3·4	0·94	0·91	1·73	1·39	0·85	0·77
W	3·8	0·96	0·94	1·53	1·57	0·89	0·91
W	3·6	0·94	0·96	1·44	1·42	0·87	0·82
prox. range of SE for ifferences	0·2–0·3	0·02–0·04	0·04–0·06	0·07–0·10	0·10–0·15	0·03–0·05	0·05–0·08
nif. of riation‡	NS	NS	NS	***	*	*	***
centage deviation from mid-parental values§							
B×C	−6·6	−0·8	4·3	9·6*	3·0	7·5	15·3†
B×W	1·2	−0·7	0·6	−0·1	16·9*	4·1	40·9***
C×W	−0·1	−1·1	8·4†	2·3	15·8†	5·7	7·8
All crosses	−1·9	−0·8	4·3	4·0	11·8*	5·7†	20·5***
iff. (O_1–O_2) e to in-reeding (± SE)		0·03 ± 0·02		0·16 ± 0·06		0·08 ± 0·03	

Significance levels in this and subsequent Tables: NS = P > 0·1; † P < 0·1; * P < 0·05; ** P < 0·01; P < 0·001.

‡ The probability of finding differences among the 'breeds' (or classes) as great as those observed if ce alone were responsible.

§ For deviations of crosses from mid-parental levels, or of all crosses from level of all purebreds ficance was tested for the actual deviations prior to conversion to percentages.

the mean of their parental breeds, the difference being greatest for the Blackface × Cheviot crosses. By weaning the Blackface had changed place with the Cheviot as the heaviest of the pure breeds and the crossbred advantage remained proportionately about the same. The ratio of weaning weight to birth weight, when analysed as a separate trait, showed significant variation among the 'breeds'. Adjusted to the basis of single lambs, the Blackface increased their birth weight about eight-fold and Cheviots about seven-fold. Inbreeding lowered both birth and weaning weights but had very little effect on the magnitude of 'breed' differences or on the weight of

crosses relative to purebreds. (There was no significant 'breed' × phase interaction.)

Litter weight at weaning. This has been analysed as a trait per ewe present at the start (193 ewes) and has also been examined as a function of ewes mated (705 records) and of ewes lambing (679 records). In the 'direct' estimates shown in Table 4, with data adjusted to offspring born to unrelated sires (non-inbred), the weight of fostered lambs are attributed to their foster mother.

As expected from the component traits, 'breed' variation was highly significant. Crossbred ewes, though better on average than mid-parental

TABLE 3

Effect of breed, crossbreeding and phase (of sire) on weights (kg) of lambs at birth and weaning and on growth

	Birth wt per lamb born		Wean. wt per lamb weaned		Ratio wean. wt to birth wt per lamb weaned	
	O_1 sire	O_2 sire	O_1 sire	O_2 sire	O_1 sire	O_2 sire
of records	786	366	700	303	700	303
'ed'						
Blackface (B)	4·06	3·73	32·0	30·6	7·85	8·08
Cheviot (C)	4·23	3·95	30·2	28·0	7·11	6·92
Welsh (W)	3·10	2·90	24·3	21·2	7·78	7·41
B×C	4·27	4·09	32·1	30·1	7·59	7·59
B×W	3·77	3·53	29·1	26·3	7·74	7·41
C×W	3·71	3·56	28·0	26·2	7·51	7·27
pprox. range of SE for differences	0·07–0·09	0·10–0·15	0·5–0·7	0·7–1·2	0·06–0·09	0·11–0·17
gnif. of variation‡	***	***	***	***	***	*
ntage deviation from mid-parental value§						
B×C	3·1*	6·6**	3·2*	2·9	1·5	1·2
B×W	5·5***	6·6**	3·6*	1·5	−1·0	−4·3
C×W	1·2	4·2	2·9†	6·8*	0·9	1·4
All crosses	3·2**	5·8**	3·2**	3·7†	0·4	−0·7
iff. (O_1–O_2) due to breeding (± SE)	0·23 ± 0·05		2·22 ± 0·37		0·15 ± 0·11	

‡ § See Table 2 for footnotes.

levels, did not exceed the production of the Blackface. The lifetime results particularly for the Blackface-Cheviot cross were handicapped, however, by the relatively high losses among ewes of this cross even though these losses may have been due to chance (see Table 2). Per lambing record, the crossbred advantage was more apparent. A second set of results shown in Table 4 provides 'indirect' estimates of litter weights by combining the component traits in such a way that fosterlings are treated as though they had been reared by the 'breed' of their natural mother. Since crossbred ewes had more lambs taken away from them for fostering than they received in return their advantage relative to the pure breeds increased by relating lambs to their natural mother.

For lifetime production of weight of lambs weaned, both the direct and

indirect estimates show the Blackface to have been best and all crossbreds to have exceeded the performance of both the Cheviot and the Welsh, although the two ways of looking at the data show differences in ranking of the 'breeds'.

Lambing date. 'Breeds' differed little in their date of lambing, the Blackface being the first and Welsh and Cheviot-Welsh the last group, less than 4 days later. The 'breed' variation was, however, statistically significant ($P<0{\cdot}02$). The phase of ram to which a ewe was mated did not affect this trait, although an effect might have been expected since the two phases of

TABLE 4

Effect of breed and crossbreeding on litter weight (kg) (a) per ewe's lambing record and (b) per lifetime (up to 5½ years old) for each ewe present at the start of the experiment. 'Direct' and 'indirect' values given as least squares estimates adjusted to the use of O_1 sires (to produce non-inbred lambs) and to 'average' parity and sex

	Litter weight at weaning per lambing record		Total litter weight at weaning per lifetime of ewe at start	
	'Direct'‖	'Indirect'‖	'Direct'‖	'Indirect'‖
'Breed'				
Blackface (B)	45·5	48·0	180·9	180·2
Cheviot (C)	36·8	36·5	136·9	122·7
Welsh (W)	32·0	32·4	124·3	118·4
B × C	45·1	50·1	158·8	165·3
B × W	41·8	43·1	163·1	160·1
C × W	37·0	38·4	138·1	133·0
Approx. range of SE for differences	2·4–3·0		13·0–16·5	
Signif. of variation‡	***		**	
Percentage deviation from mid-parental values§				
of B × C	9·6†	18·6	−0·1	9·1
B × W	7·9	7·2	6·7	8·2
C × W	7·6	11·5	5·6	11·6
All crosses	8·4*	12·6	4·0	8·8

‡ § See Table 2 for footnotes.

‖ 'Direct' estimates attribute fostered lambs to breed of foster mother. 'Indirect' estimates were calculated by combining component traits and fostered lambs are attributed to the breed of their natural mother (no test for significance of variation or of heterosis made).

ram differed in age (male lambs might have served less successfully than older rams) and their offspring differed in inbreeding.

Other factors

Parity effects. These are shown in Table 5 in respect of the 705 mating records for a number of aspects of performance. Weaning data include fosterlings but it is difficult to assess whether this has affected the result, since each group was not equally involved in fostering. As expected, production at first parity (2-year-old females) was lower than later, although there is an indication that by the fourth parity performance was beginning to decline (however, the fostering of lambs discriminated slightly against

the oldest ewes in the data at weaning). There was no significant effect of parity on the proportion of ewes lambing per mating record. Table 6 shows corresponding results for data from lambs born and weaned, although in this case age of dam rather than parity has been used. Lamb survival did not differ significantly among ages of dam, but birth weight (adjusted to singles) was less from 2-year-old (1st parity) dams and weaning weight was also fractionally lower.

TABLE 5

Effect of parity on maternal performance of ewes in relation to numbers mated

	No.	No. born	No. weaned	Litter wt at birth (kg)	Litter wt at weaning (kg)
Parity 1	202	1·70	1·38	5·76	40·7
Deviations from parity 1					
of parity 2	184	0·29 ± 0·076	0·35 ± 0·084	1·36 ± 0·27	9·9 ± 2·2
3	174	0·32 ± 0·095	0·27 ± 0·105	1·48 ± 0·33	8·6 ± 2·7
4	145	0·24 ± 0·105	0·21 ± 0·116	1·30 ± 0·37	5·2 ± 3·0
Signif. of variation‡		**	***	***	***

‡ See Table 2 for footnote.

TABLE 6

Effect of age of dam on survival and weights (kg) of lambs
(Fitted means and deviations ± SE)

	Per lamb born			Per lamb weaned	
Age of dam (yr)	No.	Survival	Birth weight (kg)	No.	Weaning weight (kg)
2	275	0·819 —	4·06 —	256	32·0 —
Deviation from 2-yr-old					
dam of 3	313	0·028 ± 0·034	0·33 ± 0·057	283	1·11 ± 0·42
4	294	−0·045 ± 0·042	0·39 ± 0·070	238	1·72 ± 0·53
5	270	−0·033 ± 0·047	0·43 ± 0·079	226	0·46 ± 0·59
Signif. of variation‡		NS	***		**

‡ See Table 2 for footnote.

Birth type, rearing and sex effects. These are shown in Table 7. Surprisingly survival of twin lambs was better than that of singles, but triplets fared worst. There was a residual correlation (equivalent to the correlation within subclasses) of 0·1 ($P < 0·001$) between birth weight and survival. In relation to birth type and rearing, birth weights and weaning weights ranked in the expected order. Ewes giving birth to singles were 2 kg lighter than those giving birth to twins and 5 kg lighter than triplet-bearing ewes when approximately 6 weeks pregnant (in January).

Males were significantly heavier at birth and at weaning than females. They had a marginally poorer survival rate after birth but the difference was not significant.

TABLE 7

Effects on lambs of sex and birth type on birth weight and survival to weaning and of sex, birth type and rearing on weaning weight
(*Fitted means and deviations* ± SE)

	(*a*) Lambs at birth			(*b*) Lambs at weaning		
	No.	Birth wt (kg)	Survival		No.	Weaning wt (kg)
ted mean‡	—	4·05	0·819	Fitted mean‡	—	32·0
viation of				Deviation of		
emale	579	— —	— —	female	507	— —
ale	573	0·25 ± 0·03	−0·015 ± 0·019	male	496	2·7 ± 0·2
irth type				birth type and rearing§		
single	202	— —	— —	single born single reared	166	— —
twin	872	−0·75 ± 0·05	0·081 ± 0·027	twin or triplet born single reared	54	−2·7 ± 0·6
triplet	78	−1·40 ± 0·08	−0·121 ± 0·047	twin or triplet born twin reared	742	−5·3 ± 0·4

‡ Fitted mean for Blackface breed (O_1 sires).
§ Reared by own dam (other categories not shown).

DISCUSSION

Among the three pure breeds the Scottish Blackface gave birth to most lambs per ewe and provided the heaviest weaning weights and lifetime output—all markedly better than the Cheviot, a breed which, on this farm, had a similar mature size (Wiener and Hayter, 1974). The Welsh Mountain, which had a mature weight 30% lighter than that of the Blackface, produced, not unexpectedly, less in absolute terms, but did not lag far behind the Blackface in overall output when related to maternal weight (or weight$^{0·73}$), which may be relevant in a consideration of relative maternal costs of producing lambs. In general, the ranking of these breeds in terms of their maternal performance agrees with the published results for the parents of these sheep (Wiener, 1967). In detailed terms, however, there are some differences, but since in the earlier study there was some confounding of breed with possible differences in treatment in the first 5 months of life of the sheep, the present study provides the more valid breed comparison. The Blackface was also reported by Gunn (1967) to have a better reproductive performance than the Cheviot when compared in a hill environment. Donald *et al.* (1963) compared Blackface with Swaledale ewes and found that over a 3-year period on a hill grazing the former produced more and slightly heavier lambs than the latter.

The Blackface also exceeded the crosses in total output although the Blackface-Cheviot cross was better in some of the component traits. The lifetime production of the Blackface-Cheviot cross, however, was handicapped by having the highest proportion of ewe deaths. Since variation for this trait among the breeds and crosses was not significant, the component traits, ignoring ewe deaths, may provide a better indication of the relative merits of the Blackface-Cheviot cross. All the crosses, however, excelled

both the Cheviot and Welsh in absolute terms and, for the most part, in relation to mature metabolic weight ($kg^{0.73}$).

Although crosses, on average, showed an advantage over the mean of the pure breeds, there were sufficient differences in the degree of heterosis shown by the three crosses to suggest that specific combining ability may be important. Litter size (per ewe lambing), for example, showed no advantage for one cross (Blackface-Welsh) and almost 10% for another (Blackface-Cheviot). Closest to showing a uniform, general heterotic effect was weaning weight per lamb (average 3·2%) followed by lamb survival (average 5·9%).

Published literature provides further evidence of the diverse consequences of crossing different breeds as also noted by Burgkart and Averdunk (1969) although, in general, heterosis is more commonly found for traits involving reproduction and survival than for other traits such as body size (see Wiener and Hayter, 1974). Comparison of the results in the literature is made difficult by the lack of uniformity in the criteria used for recording reproductive performance and survival. Even so the number of criteria and combinations recorded are only a fraction of the possible number proposed in the highly relevant review of Turner (1969). Since, however, so few of the many studies involving crossbred sheep are designed to provide information on the presence or absence of heterosis, the most relevant ones, and the breeds involved, are worth listing. They include the studies of Botkin and Paules (1965) involving Corriedale and Suffolk breeds; Donald *et al.* (1963) with Scottish Blackface and Swaledale; Fahmy and Bernard (1973) with Oxford Down, Suffolk and Cheviot; Galal, Aboul-Naga, Eltawil and Khishin (1972) with Barki, Ossimi and Mutton Merino; Iwan, Jefferies and Turner (1971) with Merino and Corriedale; Land, Russell and Donald (1974) with Finnish Landrace and Merino; McGuirk (1967) with Border Leicester and Merino; Sidwell, Everson and Terrill (1962) and Sidwell and Miller (1971a and b) with a variety of breeds including Hampshire, Shropshire, Suffolk, Dorset, Merino and Targhee; and Singh, Rempel, Reimer, Hanke, Miller and Salmela (1967) with Hampshire, Suffolk and a number of Minnesota lines of sheep. Earlier references were included in the review by Rae (1952) and additional references to crossbred performance were given by Turner (1969).

In this literature, estimates of heterosis vary from zero to 50% of the parental mean for the variety of traits and breed combinations. Some of the highest values, such as that of McGuirk (1967), involve the apparent failure of one of the breeds involved in the cross to perform 'normally' as a pure breed. As argued by Land *et al.* (1974), the source of the heterosis may be irrelevant in practical terms, but none the less an explanation based on genotype-environment interaction lessens the general applicability of the results. The results from the literature also provide conflicting evidence for the view that breeds developed in similar conditions will, when crossed, show less heterosis than those with widely differing origins or widely differing performances. Thus the Finnish Landrace × Tasmanian Merino crosses of Land *et al.* (1974) showed a marked heterotic effect in the ability to have lambs at 1 year of age (in which the Merino failed) but no heterosis for litter size for ewes which lambed at second or later parities, although the two pure breeds differed widely. By contrast, the Scottish Blackface and Swaledale of Donald *et al.* (1963) whilst remarkably alike as pure breeds displayed a little heterosis on crossing, including heterosis for the number

of lambs weaned per ewe mated, although less than the deviation observed in the present experiment.

It is not intended in this paper to discuss, in detail, the effects of the inbreeding which represents only the first stage of continuing close inbreeding in this experiment. However, both crossing of breeds and inbreeding can be expected to affect levels of heterozygosity. To the extent to which these levels are reflected in the levels of performance, the observed heterosis for any trait cannot be considered in isolation from the consequences of inbreeding.

The theoretical expectation, applying to the particular experimental design used here, is that the excess of heterozygous loci in crosses relative to the parental pure breeds should be the same irrespective of the phase of mate (O_1 or O_2) (Susan Hayter, unpublished work). Given dominance, therefore, the deviation $BC-\frac{1}{2}(B+C)$ (for example) might be expected to be the same for O_1 or O_2 mates. The crossbred deviation in the performance of several of the traits, however, was greater when the inbred progeny were produced. Clearly, the one set of deviations may be too small as readily as the other set may be too large. It seemed inappropriate, however, to pool the estimates of heterosis from the two sets of matings not least because the effects of inbreeding (of the lamb) differed among the 'breeds', particularly for litter size and lamb survival.

The assumption that the level of heterosis will reflect the excess of heterozygous loci may, however, be too simple. It ignores the possible effect of interactions including epistasis. The advantage of heterozygosity might change with the 'total amount' of it present. Inbreeding is expected to produce a reduction in heterozygosity (e.g. see Falconer, 1961). Thus the relatively greater heterosis observed when inbred lambs were born might indicate the operation of a threshold level of heterozygosity below which performance declines beyond expectation. This could be related to the environment in which the sheep are kept and it is noteworthy that Doney (1966) observed a dramatically greater reduction in reproduction and survival from inbreeding in a very much harsher environment than here.

Comparison of the magnitude of the initial inbreeding depression with the observed heterosis in the present experiment provides a preliminary indication that there may be a considerable amount of heterozygosity and non-additive genetic variation for some of the traits within these pure breeds, while the pure breeds themselves may vary relatively little from each other in gene frequencies. Later stages of the experiment are intended to provide more guidance on this point.

From among the non-genetic factors affecting maternal performance shown in the results, attention should be drawn to the significantly better survival, from birth to weaning, of twin lambs compared with singles. This does not conflict with the observation in the earlier, parental, generation in the same flock (Wiener, 1967) where survival of the two types of lamb was almost the same, but it is at variance with the more commonly recorded observation that twins survive less well than singles (e.g. Purser and Young, 1964; Bichard and Cooper, 1966). Recently, however, better survival of twin lambs than of singles has been reported in respect of Dorset Horn and Dorset Down flocks (Cappon, 1972). For the Dorset Horn, the higher mortality among singles was thought to be associated with their large size at birth relative to twins. A similar explanation is unlikely to apply to the present study.

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DISTRIBUTION OF PEDIGREE AYRSHIRE, BRITISH FRIESIAN, AND SHORTHORN CATTLE IN GREAT BRITAIN IN RELATION TO TEMPERATURE AND RAINFALL

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THE three breeds of dairy cattle which were in 1946 numerically the most important in Great Britain, Ayrshires, Friesians, and Shorthorns, were distributed over most parts of the British Isles. Each breed is thus found under a variety of different environments, some of which may favour one breed more than another. The purpose of this paper is to discuss whether the relative proportions of the three breeds to each other within the different districts can be related to climatic variations. An attempt has also been made to ascertain whether differences in milk yield between districts and between breeds can be related to the criterion of environment used.

Average temperature and rainfall over the relatively large areas of the meteorological districts [1] into which Great Britain has been divided are used as the environmental 'factors'. The underlying assumption is that climate, though represented in this rough manner, may affect even individual herd management, either directly, or indirectly through land utilization and the vegetation.

Most of the work done in the past on animal-environment relationships has dealt with environments differing very widely from that native to the animal or breed, and has applied to single animals or herds, e.g. temperate-zone cattle and sheep for Mediterranean or tropical climates [2–7]. Extensive lists of references are found in reviews by Hammond *et al.* [8], and by Phillips [9]. Studies involving whole breeds have been made by Johnson [10] and Davidson [11] on sheep and cattle distribution in the U.S.A., and by Nichols [12] for sheep in Britain.

Material and methods.—The material is the distribution of registered herds and registered females in vol. 69 (1946) of the *Ayrshire Cattle Herd Book*, in vol. 35 (1945) of the *British Friesian Herd Book*, and in vol. 91 (1945) of *Coates's (Shorthorn) Herd Book*. Only England and Wales are dealt with in this study (except for Ayrshires) because over 90 per cent. of the Friesian herds and females registered in Great Britain are found in England and Wales, and because the majority of Shorthorn cattle in Scotland are of the beef, not the dairy, type. The cattle distributions have been related to 7 of the 12 districts of the British Isles given in the *Book of Normals* published in 1920 by the Air Ministry Meteorological Office [1]. This book gives the mean monthly temperature and the mean monthly rainfall for each of the 12 districts referred to. The means are for the period 1881–1915 (used as the 'standards' for meteorological work). Taking each district separately, the mean monthly

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temperature was plotted on a graph (vertical axis) against the mean monthly rainfall (horizontal axis) after the hythergraph method of Taylor [13]. On the resulting polygon, a big vertical distance between the extremes shows a wide variation of mean monthly temperature between hottest and coldest month, and the longer the horizontal distance between the extremes of the hythergraph, the greater the difference of mean monthly rainfall between driest and wettest month of the year (a single dot would indicate that precisely the same monthly mean of temperature and of rainfall prevail in every month of the year).

Temperature and rainfall range for the county of Ayr (referred to in the Discussion) was obtained by using climatological summaries for the years 1932–49 for 4 stations in Ayrshire: Auchincruive, Kilmarnock, Prestwick, and Turnberry, for each of which both the highest and the lowest monthly mean temperature and total monthly rainfall that had obtained in any of the 18 years was noted. The lowest figures from each station were then averaged, giving an 'average lowest', and the highest were similarly arranged to give an 'average highest'. The reason for this was to smooth out such extremes of monthly mean as had obtained perhaps only once in the course of 18 years at one of the stations. The resultant range of 'average lowest' to 'average highest' was thought to be more akin to a range for the whole of that part of the county of Ayr where Ayrshire cattle originated and are densest.

Milk records were obtained for breeds and by counties from the annual reports for the year ending October 1, 1946, of the National Milk Records of the Milk Marketing Board [14]. The breed averages were calculated from county herd averages (given separately for each breed) and weighted for number of herds; they differ slightly from the average given by the National Milk Records, which are weighted for numbers of cows.

Hythergraphs for districts of the British Isles.—These are the polygons shown in Fig. 1 for 7 districts comprising the whole of England and Wales, and the West of Scotland. The hythergraphs show that rainfall, as average monthly means, varies more from district to district than does temperature. No month in districts 2, 3, and 4 shows a rainfall of over 3 in., whilst in District 6 only 3 months have less than this. Shapes of hythergraphs for the 7 districts studied can be seen to vary appreciably from the long thin type (district 3) to the broad and short type (district 8). The assumption underlying the use of these hythergraphs is that their shape is characteristic of the climate—as represented by temperature and rainfall—for their districts; and as there may be a correlation between breed distribution and climate, there may also be one between breed distribution and shape of hythergraph.

Distribution of Pedigree Ayrshire, Friesian, and Shorthorn Females—according to Meteorological Districts and in relation to Hythergraphs

The actual numerical distribution of the registered females of these breeds is not given here, because, as stated in the introduction, primary interest centres around the question whether the climate of any district has favoured one breed rather than another. To this end the breed data were converted to a percentage basis, and expressed for each breed as a

percentage of the total registered females of the three breeds combined in each district; this is shown in Table 1, and in Fig. 1.

If the proportions of the three breeds to each other in England and

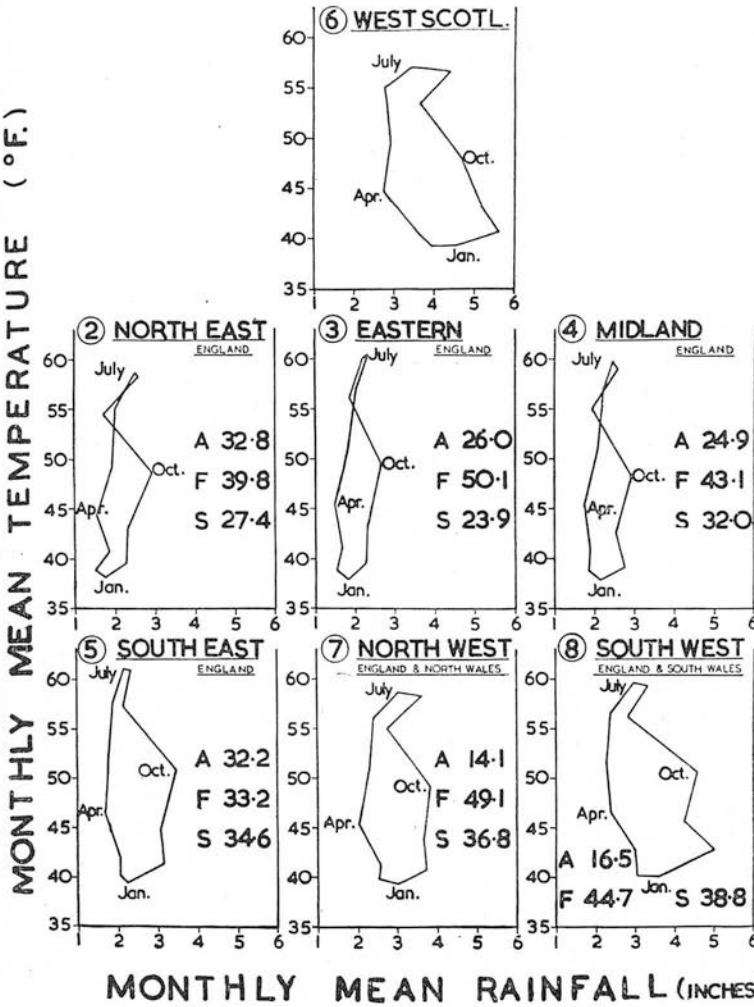

FIG. 1. Hythergraphs for seven districts of Great Britain. The figures alongside the hythergraphs show the number of Ayrshire (A), Friesian (F), and Shorthorn (S) heifers registered in 1945–6 as a percentage of all registrations of heifers of these three breeds.

Wales as a whole (24·0, 43·5, 32·5) were accepted as the proportions to be expected in each district—provided the same factors operate in each district as they do in the country as a whole—then the variable proportions in fact found might be used as a measure of inter-breed competition. The reasons for the relative success or failure of one breed in relation to others may derive from a variety and combination of causes, genetic,

environmental, economic, or due to local reputation of the breed for some other reason. The importance of any one factor may vary from district to district, and from time to time; the purpose here is only to ascertain whether climate has had any recognizable effect.

TABLE 1. *Percentage Distribution of Heifers of Three Breeds of Cattle Registered in 1945–46 in each of Six Meteorological Districts of England and Wales*

Meteorological district	*Total registered ♀♀ in each district for three breeds combined*	% *Ayrshires*	% *Friesians*	% *Shorthorns*
2. England NE. . .	2,283	32·8	39·8	27·4
3. ,, E. . .	5,118	26·0	50·1	23·9
4. ,, Midlands .	10,375	24·9*	43·1*	32·0*
5. ,, SE. . .	5,534	32·2	33·2	34·6
7*a* and *b*. NW. England, N. Wales . .	5,538	14·1	49·1	36·8
8*a* and *b*. SW. England, S. Wales. . .	4,177	16·5	44·7*	38·8
England and Wales: Total . . .	33,025	24·0	43·5	32·5

* Percentages marked with asterisk do not differ significantly (P = 0·01) from percentages based on totals; all others do (significance calculated on numbers of registrations 'expected' in each district, not on percentages given above).

It might be that a breed of livestock when it enters new territory succeeds best in relation to other breeds, and becomes most numerous in those districts which are climatically most similar to its native region—other things being equal. If this were true, and if shape and range of hythergraphs represented climates, one would expect pedigree Ayrshire cattle to have succeeded best in relation to other breeds in districts of England and Wales which show hythergraphs most akin in range and shape to that of the West of Scotland (district 6). The districts most nearly approaching such similarity with the West of Scotland are the South-west of England and South Wales (district 8) and the North-west of England and North Wales (district 7). But these are just the districts where Ayrshires are numerically weakest in relation to the other two breeds. Conversely, district 2 (NE. England) where Ayrshires have succeeded best relative to the other breeds, has a hythergraph most unlike both in range and shape that of the home of the breed (district 6).

Friesians are seen to be most numerous relative to the other two breeds in districts 3 and 7, yet the hythergraphs for the two districts differ appreciably within the range found in England and Wales. The proportion of Shorthorns, relative to the other two breeds, increases with increasing average annual rainfall—particularly winter rainfall (October–March)—from district to district. The order of the districts according to increasing average annual rainfall, and average winter rainfall, is 3, 2, 4, 5, 7, 8; this is also the order from lowest to highest in the proportion

of Shorthorns to other breeds found in these districts. One is led to speculate whether this is coincidence, or whether farmers do in fact prefer Shorthorns to either Ayrshires or Friesians for the wetter winter conditions. For Ayrshires this would appear anomalous, as the average rainfall in the West of Scotland, where Ayrshires originated, is higher than in any of the English districts. It may be, however, that in England and Wales, at least, there is a difference of purpose on the part of the Shorthorn breeders on the one hand, and of Friesian and Ayrshire breeders on the other. One breed may be treated as dual purpose to be kept under extensive conditions, the other as single purpose for intensive management. If it were found that Shorthorn numbers have declined most in the drier districts of the country, it would be more concrete evidence than that presented; it may be worth investigating this point further.

Milk Yield according to Breeds and Meteorological Districts

Although climatic differences (as represented by hythergraphs) exist between meteorological districts of the British Isles (*v.s.*), it would be difficult to decide from the evidence whether these differences have in part determined the breed distributions. It may be, however, that the differences in climate can be related to differences in milk production between districts and breeds.

The milk yields—quoted here as average herd yield of milk in lb.—published by the Milk Marketing Board [14] are for pedigree and non-pedigree stock combined; the data should not therefore be strictly related to the distributions of pedigree Ayrshires, Friesians, and Shorthorns given earlier in this paper. The average yield for each meteorological district and for each breed was calculated from the county data: the whole of Yorkshire was for this purpose included in district 2 (NE. England). The total number of herds recorded in England and Wales for the year ending October 1, 1946, were 1,303 Ayrshire, 2,722 Friesian, and 5,023 Shorthorn.

Fig. 2 shows that in all 6 meteorological districts of England and Wales, the recorded herds of Friesians had the highest average yield, and the Shorthorns the lowest. Moreover, the differences in yield between the breeds appear to have been very similar in each of the 6 districts. There are also differences in average yield of breeds between the districts, but the order of yield between districts is almost the same for each of the 3 breeds. Arranged from highest to lowest according to average yield these 6 meteorological districts read: 3, East of England; 5, SE. England; 4, Midlands; 8, SW. England and S. Wales, 2, NE. England, and 7 NW. England and N. Wales. The only deviation from this order is a reversal of order of districts 4 and 5 for Friesians, whose average yield in district 4 was 8,532 lb. and 8,497 lb. in district 5. The difference in average yield between highest and lowest district was 1,559 lb. of milk for Friesians, 1,431 lb. for Ayrshires, and 1,481 lb. for Shorthorns. These findings are in general accord with those of Edwards [15], who noted that Shorthorn and Friesian yields were affected similarly by districts, and that yields decreased from east to west of England.

The rank in yield of the districts does not, however, appear to be related either to the rank of rainfall or to that of average temperature as shown by the hythergraphs. It is true that the highest-yielding district—

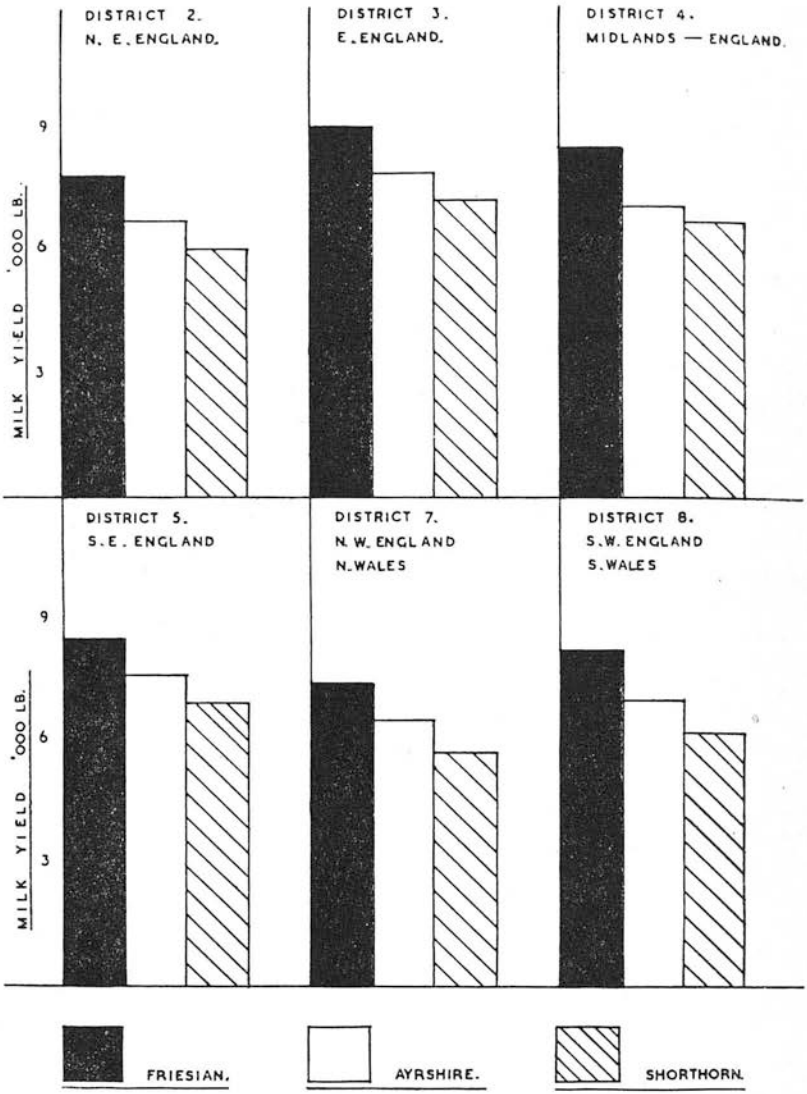

FIG. 2. Average milk yield (lb.) of recorded herds of the Friesian, Ayrshire, and Shorthorn breeds of cattle in 1945–6 in six meteorological districts of England and Wales.

East of England—also has the lowest average monthly rainfall, which may be of advantage; similarly the two districts (Nos. 2 and 7) with lowest average yield have the lowest average monthly temperature in April and May and again in September. This might affect the length of

the grazing season. The amounts in average monthly rainfall and in average temperature which separate the districts are, however, so small that it would be wrong to read any significance into these slight associations between yield and climate.

Discussion

The approach used in this paper to the problem of breed distribution in relation to climate might be criticized on at least three considerations:

1. The pedigree female population may not be representative of the total population for each of the three breeds.
2. The districts used vary in size.
3. The hythergraphs for the present purposes might be irrelevant.

That registered females of each breed may not be representative of the total population of that breed is largely irrelevant here, because in studying the registered populations only, fair comparison is being made between the portions of each breed which will contribute most genetically to the future generations of their respective populations.

The fact that districts vary in size cannot be ignored. On the one hand, the larger the district the greater the chance for internal temperature and rainfall variations, and the less representative is any average figure of conditions in any part of a large area. On the other hand, the districts were chosen by the Meteorological Office in part, no doubt, as climatic entities, not only as geographic ones. Size of district may, of course, of itself influence the proportion of the total pedigree population of any breed that is found in the district, but this should not affect the inter-breed relationship as used here.

The data presented are considered to be only crude approximations, but the conclusion seems warranted that temperature and rainfall in themselves—within the range found in England and Wales—have played little part in determining the numerical relations of the three breeds of cattle—although an indication that rainfall may play some part was indicated by the relationship of increasing rainfall and increasing Shorthorn proportion shown earlier. The Ayrshire breed does not appear to have succeeded best in relation to the other two breeds in districts of England and Wales showing the greatest climatic affinity with its native area—climate, that is, as represented by the hythergraphs.

These mainly negative conclusions are not very surprising if the range of mean monthly temperature and monthly rainfall is considered over a period of time. Thus it can be shown by the procedure described under 'Material and Methods' that the range of monthly mean temperature and monthly rainfall that had obtained over 18 years in the county of Ayr, includes all the extreme points of monthly means as shown in the *Book of Normals* for all the major districts for which hythergraphs were drawn.

It was stated earlier that observed differences in average milk yield between districts cannot, with any confidence, be related to climatic differences as shown by the hythergraphs. Temperature and rainfall, and therefore hythergraphs, are not, of course, the whole of the climatic story of any district. Thus, Lee and Phillips [16] list no less than five

climatic elements each related to animal production: viz. temperature, humidity, air-movement, solar radiation, and altitude. If, however, the meteorological districts could be regarded as environmental 'entities', in a broad sense, the higher or lower yield of a breed according to district might be an adaptive response of the breed to its environment. This could lead to the formation of local breed-types in response to selection by—or because of—the environment, if other conditions relating to the size of the population and the interchange of breeding-stock between districts are met. Within the three breeds of cattle considered in this paper, no differentiation of local types can be postulated because of a large amount of migration within each breed [17, 18].

If it can be assumed that differences in average milk yield that exist between breeds indicate differences in genotype of these breeds in respect of milk yield, then the data presented in Fig. 2 show that there has been no genotype-environment interaction (environment defined here by districts). The three breeds are seen to behave similarly in respect of milk yield according to district.

This absence of interaction is brought out by Table 2, which shows for each district the breed-yield relative to the average yield of recorded herds of that breed in England and Wales as a whole. The average breed-yields (England and Wales) were designated 100 per cent. for each of the three breeds. In the highest-yielding district (No. 3) the recorded Friesians yielded 108·6 per cent. of their national average, Ayrshires 111·6 per cent., and Shorthorns 111·8 per cent. The relative yields of recorded herds in the lowest-yielding district (No. 7) were 89·9, 91·6, and 89·0 per cent. respectively. The table shows that there were differences of about 20 per cent. between the relative yields in highest and lowest district, but that these differences were equally reflected by all three breeds.

TABLE 2. *Relative Milk Yield of Recorded Herds of the Ayrshire, Friesian, and Shorthorn Breeds of Cattle in 1945–6 in six Meteorological Districts of England and Wales (yields adapted from M.M.B. data)*

	Ayrshires		*British Friesians*		*Shorthorns*	
Meteorological district	*No. of herds*	*District yield as % of average breed-yield*	*No. of herds*	*District yield as % of average breed-yield*	*No. of herds*	*District yield as % of average breed-yield*
2. England NE. .	222	95·8	353	94·7	550	93·7
3. England E. .	157	111·6	482	108·6	435	111·8
4. England Midlands . .	332	100·0	771	102·6	1,123	104·4
5. England SE. .	207	106·1	260	102·2	934	106·4
7. England NW. and N. Wales	229	91·6	427	89·8	732	89·0
8. England SW. and S. Wales	156	98·7	429	98·9	1,249	96·4
England and Wales total herds and average yield of milk (lb.) .	1,303	7,156	2,722	8,315	5,023	6,505

The fact that these yield-differences cannot be ascribed to either temperature or rainfall variation between districts, or to a combination of the two, as shown by the hythergraphs, indicates that either these factors are of little significance in causing these variations, or the hythergraph method is inefficient when applied, as here, to districts which are large relative to the total area of breed-distribution involved, and when climatic variation between districts is not great.

Summary.—Hythergraphs are used to show temperature and rainfall variation from district to district for the six meteorological districts of England and Wales and for the West of Scotland. Alongside the hythergraphs is shown the proportion in each district of pedigree Ayrshire, Friesian, and Shorthorn cattle. It is shown that the proportion of Shorthorns to the other two breeds increases with increasing average winter rainfall (and average annual rainfall) of the districts, but this cannot be accepted as conclusive evidence that, of the three breeds, Shorthorns are preferred for the wetter climatic conditions. There appear to be no other clear associations between breed distribution and climate. Ayrshires have not succeeded best in relation to the other breeds in districts of England and Wales showing closest similarity in climate with the West of Scotland, where Ayrshires originated.

A weakness of the hythergraph method in this investigation lies in that mean temperature and rainfall data for the 35-year period given in the *Book of Normals* hide variation. The range of means during an 18-year period in the county of Ayr alone includes all the extreme points of monthly means based on the 35-year period for all the major districts of the hythergraphs.

The East–West trend of declining milk yield is shown for the Ayrshire, Friesian, and Shorthorn breeds of cattle according to the six meteorological districts. The rank in yield of the districts does not appear to be related either to rank of rainfall or to that of temperature as shown by the hythergraphs. District affects similarly the milk yield of each of the three breeds; there has thus been no genotype environment interaction (genotype defined here by breed, and environment by district).

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GROWTH OF THE PEDIGREE AYRSHIRE CATTLE POPULATION IN GREAT BRITAIN

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IN the realm of live-stock improvement emphasis is receding steadily from the small unit of the single individual and the single herd and is turning to the larger units of regional groups within breeds of live-stock and to breeds, or even species, as a whole. It follows the statistical nature of heredity that, in general, the larger the unit of material (herd, regional group, population, &c.) the more closely will it conform both under static and under changing conditions to patterns predictable by statistical techniques. In order to formulate breeding plans, it is, however, first necessary to know what is the present structure of the population to be planned for, and how this structure has changed over a period of time. The account which follows is intended to contribute information on some aspects of the dynamics of the Ayrshire cattle population in Great Britain.

Early history.—When in 1811 Aiton [1] published his *General View of the County of Ayr*, he noted an 'Adage of the district of unknown antiquity: "Kyle for a Man, Carrick for a Cow, Cunningham for Butter and Cheese, and Galloway for Woo".' From this it would appear that the Cunningham district of Ayrshire had for long been renowned for its milk cattle, though it seems reasonable to suppose from the evidence of other authorities, quoted by Prentice [2], that this renown does not date back much farther than the end of the seventeenth century. Douglas [3], Smith [4], and Prentice [2] give admirable summaries of the breed history, and the account of Farrel [5] published in 1876, though in the light of subsequent writings more speculative in its conclusions, is of interest too. The Highland and Agricultural Society of Scotland offered prizes for bulls and heifers in the Kyle district of Ayrshire in 1814, and Smith [4] states that this is the first public reference to the breed by the name of Ayrshire. The Herd Book Society was founded in 1877 and its first volume was published in 1878.

The Ayrshire breed spread more slowly at first than had been expected by Aiton [1], but Low [6] writing in 1852 states that '. . . it now forms the prevailing stock (apart from Ayrshire) of Renfrew, Dumbarton, Stirling, and Lanark, and it has extended into the shires of Dumfries, Wigtown, and Kirkcudbright. It has been carried into England, where, however, it has never arrived at the estimation which it possesses in its native pastures . . . those (cows) of Ayrshire appear to have the peculiarity of tending too much to fatten with a corresponding diminution of milk when they are transported to richer herbage than is natural to them.' The breed had, however, even then been exported to the U.S.A., Canada,

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and Finland, and, subsequently to Low's report, it went to Sweden, Norway, New Zealand, Australia, and many other parts of the world [4]. Ayrshires outside Britain appear to have been particularly successful, while retaining their breed identity, in the U.S.A., in Canada, and in Finland.

It is with the period after the establishment of the Ayrshire Herd Book in 1878 that this study deals, but it is in the light of early breed history that subsequent events may best be appreciated.

Material and methods.—The material consists of registrations of pedigree males and females, and of grade females taken from the herd-books of the Ayrshire Cattle Herd Book Society. The latest volume available when this study began was vol. 69, 1946. Although details of regulations for entry into the herd-book, and particularly into the appendixes, have altered slightly with the passage of the years, the general pattern of the information given in respect of each animal has remained much the same over the whole period of publication of the book. Registrations have been taken as indicative of population trends in the pedigree Ayrshire population. If the number of annual registrations is plotted against the appropriate years, the resulting frequency polygon shows the rate of increase and fluctuations in the size of the pedigree population (as represented by annual registrations). Examination of Fig. 5 (p. 201) will show that the six years (1879, 1896, 1906, 1927, 1943, and 1946) chosen in the following pages to study the growth of the registered Ayrshire population are fairly representative of the various periods of numerical growth. Vol. 1, 1878, had to be excluded from consideration in this study since it contains the entries of foundation animals both dead and alive, and of all ages. Age at registration has varied from period to period. The majority of animals are now registered within a few weeks of birth, but before 1914 the registrations were about equally divided among all ages up to about 4 years old. Where these differences in registration habits are likely to detract from the value of registrations as an indication of population numbers and trends, this will be stated in the appropriate section of this study.

Herds are defined (except where otherwise stated) as consisting of animals registered by owners or breeders of Ayrshire cattle who register at least one female in any volume of the herd-book under consideration. Herd sizes were calculated on the number of females registered by herd owners, who were not necessarily the mating breeders.

Although absolute accuracy of herd-book information, and particularly of pedigrees, cannot be assumed, the herd-book entries are considered a sufficiently reliable source of information for the purpose in hand, since it is the actual existence of animals, rather than their particular ancestry, that is of primary interest here.

Geographical distribution.—The location of pedigree Ayrshire herds at various periods will be found in Figs. 1–4. Each dot on the maps represents one herd irrespective of size; in view of the large number of herds involved, particularly in later years, it is not practicable to make a herd-size distinction.

In 1879, the year after the inception of the herd-book, it can be seen

that the majority of the herds are clustered in Ayrshire; most of the remaining herds are found in the adjoining counties of Lanark, Renfrew, and Dumfries. It is of interest that no females were registered from the neighbouring counties of Wigtown and Kirkcudbright—in fact if the 'geographical distribution' of the 165 members of the Herd Book Society

FIG. 1. Distribution of herds registering Ayrshire females in 1879.
(Each dot represents one herd—irrespective of size.)

in 1879 is examined, it is found that the native area and the large milk-consuming area of Glasgow and neighbourhood accounted for 90 per cent. of those interested at that time in pedigree Ayrshire cattle.

The distribution of the registered Ayrshire population had not changed much even at the turn of the century, but by 1927 the south-west of Scotland (excluding Ayrshire) had more herds of registered Ayrshires than the county of Ayr itself. Although only 39 herd owners in England and Wales in 1927 registered Ayrshire females, it can be seen that the distribution of these herds had more or less set the broad pattern of the distribution of the breed in later years. This is similar to the findings of Donald [7] with Red Poll cattle.

By 1946 there are seen to be pedigree Ayrshire herds in practically all districts normally associated with dairy cattle in England, Wales, and

Scotland, even though relative to other breeds they are more numerous in some districts than in others.

Numerical growth and features of the increase.—Pearl [8] has shown that the growth of populations in relation to their environment—like the growth of individual organisms (Brody [9])—follows a trend which can be described by an S-shaped curve. In the pedigree Ayrshire cattle

FIG. 2. Distribution of herds registering Ayrshire females in 1906.

population there was a steady increase in the number of registrations from about 1906 to 1942; rate of increase then became very rapid. This is shown by Fig. 5. The marked irregularity in the number of registrations of females at the time of the 1914–18 war is due primarily to a change in registration procedure which was abandoned again in 1920. Fluctuations in the number of registrations between 1916 and 1922 do not therefore imply corresponding fluctuations in actual population numbers. If the data for Fig. 5 are plotted on arith-log graph-paper and a straight line fitted by eye, it is found that the rate of increase is roughly exponential. If it continued, the annual number of registrations would be about 50,000 by 1960. Such extrapolation, however, presupposes a continuance of the conditions that governed the growth of the population

up to the last census. Obviously, forces must come into play sooner or later which will check the rate of expansion and ultimately limit the size of the population. From the available evidence it may be said,

FIG. 3. Distribution of herds registering Ayrshire females in 1927.

however, that this stage in the growth 'curve' of the pedigree Ayrshire cattle population in Great Britain had not been reached in 1946.

When the data are examined by regions as in Table 1, it becomes clear that breed growth has not been uniform.

It can now be seen that up to 1906 the numerical expansion of the

FIG. 4. Distribution of herds registering Ayrshire females in 1946.

TABLE 1. *Numerical Distribution of Pedigree Ayrshire Cattle according to Region in Six Representative Years*

(*Herds are defined as registering at least 1♀; ♀♀ include appendix animals*)

	1879 number of		*1896* number of		*1906* number of		*1927* number of		*1943* number of		*1946* number of	
Region	*herds*	♀♀ *reg.*	*herds*	♀♀ *reg.*	*herds*	♀♀ *reg.*	*herds*	♀♀ *reg.*	*herds*	♀♀ *reg.*	*herds*	♀♀ *reg.*
Ayrshire	28	73	62	476	88	684	134	1,621	198	3,410	299	4,591
SW. Scotland (excl. Ayr)	15	78	42	468	45	370	231	3,024	321	5,703	538	8,982
Rest of Scotland	6	16	10	38	11	63	39	278	83	1,314	214	2,871
England, Wales, and Ireland	2	3	6	28	1	4	44	420	309	4,066	897	8,226
Total	51	170	120	1,010	145	1,121	448	5,343	911	14,493	1,948	24,670

breed was confined largely to the county of Ayr itself. Between 1906 and 1927 both the absolute and the proportionate increase in numbers of herds and of females was greatest in the area surrounding the county of Ayr, i.e. the region termed 'SW. Scotland' in Table 1 (this region includes the counties of Bute, Dumfries, Kirkcudbright, Lanark, Renfrew, and Wigtown). In the period 1927–43 the greatest proportional

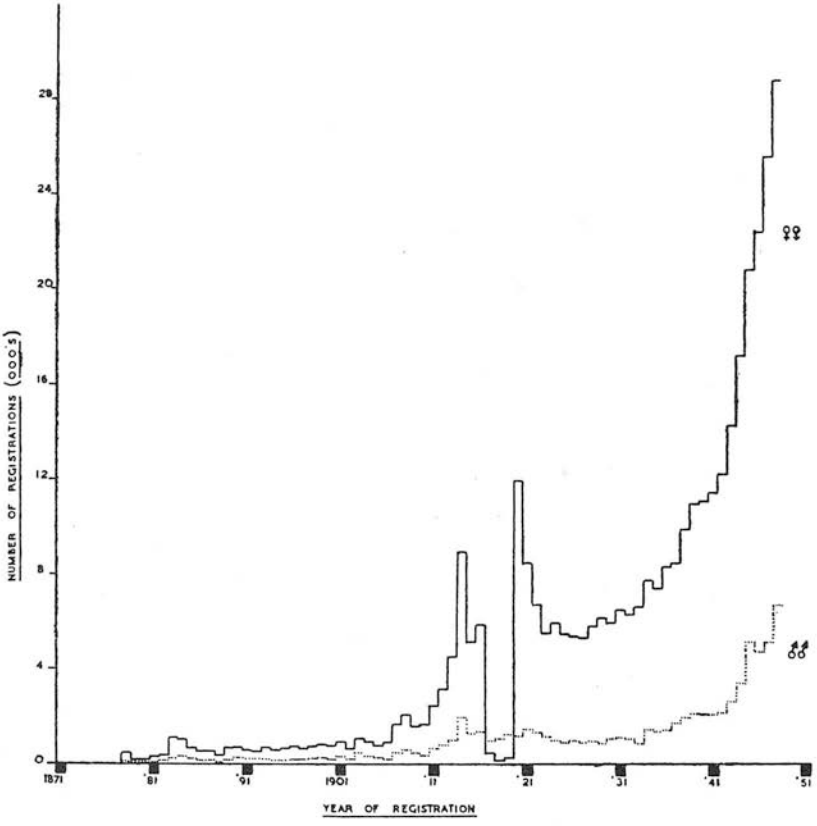

FIG. 5. Annual registrations of males and females in the herd-book (excluding appendixes since vol. 1, 1878.)

increase in herds and in females took place in England, and between 1943 and 1946 again in England, but about equally in the area termed the 'Rest of Scotland'. As during each of the periods chosen since 1906 the rate of growth in number of herds (except SW. Scotland between 1927–43) and in number of females has been greater than in the preceding period, each of the four regions is still in the 'expanding' stage of the population-growth curve. This is not to say that the growth-curve looks the same for each of the regions, or that expansion will continue for the same period in all of them.

One of the features of breed expansion—particularly when this takes the breed into districts where it was not previously kept—will be the

establishment of a large number of new herds which may or may not differ in size from their older contemporaries. The importance of herd-size in live-stock improvement has been stressed by Donald and Itriby [10]: chance variations in gene-frequency are likely to be more violent and less predictable in small herds than in large ones [11]. It is worth while, therefore, to examine briefly the effect on herd-size of the Ayrshire-breed expansion. When most of the females are registered during their first year of life, an estimate of herd-size may be obtained by multiplying the number of females registered per herd by 5 [10]; this procedure would thus give an underestimate of herd-size for the first three volumes (2, 19, and 29) but not for the later three volumes (50, 66, and 69) here studied (see *Material and Methods*).

Up to 1943 the number of Ayrshire females registered increased at a greater rate than the number of herds, with a consequent rise in average herd-size (Table 2); between 1943 and 1946, however, the rate of increase in the number of herds exceeded that of females with the result that the average number of females registered per herd dropped from 15·9 to 12·7. It is not, of course, possible to say without further investigation what proportion of the registrations made in 1946 was absorbed by herds already in existence for a number of years, and what proportion can be ascribed to newly established herds. It seems reasonable to suppose, however, that under economic conditions favourable to the dairying industry, the well-established herds would at least maintain, if not increase, their size (apart from those which 'die' in the ordinary course of events). This assumption is to some extent borne out by examining the average number of females registered per herd on a regional basis; thus, Table 2 shows that the decline in the average number of females registered per herd was proportionately much smaller in the county of Ayr, an area with a large proportion of long-established herds (from 17·2 to 15·4, i.e. a reduction of slightly over 10 per cent.), than in England, Wales, and Ireland with relatively more newly established herds (from 13·2 to 9·2, i.e. a decline of over 30 per cent.).

TABLE 2. *Average Number of Females registered per Herd in Six Representative Years, according to Region*

Region	*1879*	*1896*	*1906*	*1927*	*1943*	*1946*
Ayrshire . . .	2·6	7·7	7·8	12·1	17·2	15·4
SW. Scotland (excl. Ayr)	5·2	11·1	8·2	13·1	17·8	16·7
Rest of Scotland . .	2·7	3·8	5·7	7·1	15·8	13·4
England, Wales, & Ireland	1·5	4·7	4·0	9·5	13·2	9·2
Great Britain—Average .	3·3	8·4	7·7	11·9	15·9	12·7

It will be noted, moreover, that of the four regions shown in Table 2, only England, Wales, and Ireland—the region with the largest absolute and proportionate increase in the number of herds since 1927 (see Table 1)—fails to show an increase in the average number of females registered per herd in 1946 compared with 1927. It would thus appear

that the decrease in the average number of females per herd between 1943 and 1946 is due primarily to the establishment of relatively large numbers of new herds that are smaller than their older contemporaries. This may be further substantiated if it can be assumed that herds start with small numbers which they build up gradually. Table 3 shows the change in frequency of small and of large herds over a period of time.

TABLE 3. *Average Number of Females registered per Herd in Large and Small Herds in Six Representative Years*

Year of Registration (H.-B. volume)	*Herds registering* < 10♀♀		*Herds registering* > 10♀♀	
	No. of herds	*Av. No. of ♀♀ reg. per herd*	*No. of herds*	*Av. No. of ♀♀ reg. per herd*
1879 (vol. 2)	50	2·6	1	(40)
1896 (,, 19)	83	4·2	37	17·9
1906 (,, 29)	104	4·6	41	15·7
1927 (,, 50)	229	5·6	219	18·6
1943 (,, 66)	401	4·9	510	24·6
1946 (,, 69)	1,117	4·2	831	24·1

Whilst average size of herds registering less than ten females per herd has been falling since 1927, that of herds registering more than ten females per herd has been rising (the slight decrease between 1943 and 1946 is proportionately much smaller for the large than for the small herds).

It should be added that Donald and Itriby have shown that in 1939, over 75 per cent. of herds of all dairy breeds except Ayrshires (40 per cent.) fell within the limitation of a herd size of 1–20 cows. The data in this study show in respect of herd size for Ayrshires in 1927, 1943, and 1946 broad similiarity with that of the previous study made for 1939. In 1946, 22 per cent. of the herds registering Ayrshire females belonged to a size-class exceeding 100 females of all ages (registering >20 females), and both in 1943 and in 1946 about 60 per cent. of all the females registered came from such herds.

Regionalization of bull breeding.—A widening of the geographic distribution of a breed of live-stock may mark its entry into environments different from that of its native area and may involve the development of new breeding centres adapted for possibly new requirements. Especial interest centres therefore around those herds that make the greatest contribution to future generations of the breed, i.e. the herds breeding males, and more specifically those whose males become the sires of future generations of the pedigree population.

It has been shown [12] that in the Ayrshire breed there exists a division of function amongst herds. A large proportion of the pedigree Ayrshire population was shown to have been sired by bulls from a relatively small number of herds. Not all herds bred bulls, and only a few bred them in large numbers. In Table 4 it is shown that this specialization of function has a geographic aspect: the production of sires of pedigree

stock, particularly males, is concentrated in the native area of the breed, that is, Ayrshire and the adjoining counties of the south-west of Scotland. In this Table, columns 1 and 2 show the percentage distribution—according to regions—of the female and of the male registrations made in the herd-book in 1946; thus, in 1946, herds in Ayrshire registered 18·4 per cent. of all the females and 23·5 per cent. of all the males. Column 3 of Table 4 shows the percentage distribution of a sample of registered females arranged according to the regions where their sires originated, and column 4 uses the same classification for all the males registered in the 1946 herd-book; thus 41·9 per cent. of the females in the sample and 52·7 per cent. of all the males registered in that year were sired by bulls bred in Ayrshire, compared with less than half that number registered by herds in that county.

TABLE 4. *Distribution of Females and of Males registered in 1946, according to* (i) *Region of Registration;* (ii) *Region where the Sire originated*

	Distribution according to region of registration		*Distribution according to region of origin of sire*	
	1	*2*	*3*	*4*
Region	*% of all ♀♀ registered (excluding appendixes)*	*% of all ♂♂ registered in herds registering at least 1♀*	*% of ♀♀ in the sample*	*% of all ♂♂ in the herd-book*
Ayrshire	18·4	23·5	41·9	52·7
SW. Scotland (excl. Ayr) .	35·2	27·2	35·4	27·8
Rest of Scotland . . .	11·9	11·2	5·5	3·0
England, Wales, and Ireland .	34·5	38·1	17·2	16·5
Total number . . .	22,422	4,438	2,231	4,737

Table 4 shows that in 1946, 38·1 per cent. of bulls registered were bred in England, Wales, and Ireland, but 16·5 per cent. had sires bred there. It follows that the sires of the majority must have come from Scotland.

If all the males registered in the 1946 herd-book are classified according to the herds where their sires originated, it is found that bull-breeding herds in Ayrshire each supplied the sires of an average of 26·3 males registered in the herd-book, whereas each such herd in the south-west of Scotland (excluding Ayrshire) provided the sires of 9·6 males, herds from the 'Rest of Scotland' the sires of 4·2 males, and English, Welsh, and Irish herds the sires of 5·3 registered males. There is considerable variation within regions in the number of registered males that may be traced through their sires to a particular herd. In Ayrshire, some herds were in 1946 represented by only one registered male, and two herds each by more than 300 males. It may be concluded, however, that on average the effectiveness of selection in herds in Ayrshire which supply bulls to other pedigree breeders is likely to be significant for the whole breed.

Discussion

Large expansion such as that of the Ayrshire cattle population over the past fifty years or so has at least four concomitants of interest to the geneticist:

1. Rate of increase, which influences the amount of selection that can be practised;
2. new environments and possibly geographical isolation, which may lead eventually to the development of local breed types;
3. effective size of breeding population, which will determine what changes in gene-frequency might be expected from varying degrees of selection pressure, or from random fluctuations; and
4. wider opportunities for cross-breeding.

Dawson and Graves [13], using a hypothetical case of a herd of 1,000 milking cows, assuming no culling for low producers and a 12 per cent. annual wastage-rate, calculated that the herd would double its number in seven years. Donald [14] showed that a breed would double its number of registrations in seven or eight years at a steady rate of increase of 10 per cent. per annum. The latest Ayrshire herd-book on hand (vol. 71—the second volume published in 1947) shows that Ayrshire female registrations have doubled within roughly five years. The percentage increases from 1943 to 1947 were 20, 21, 8, 14, and 13. The 12 per cent. annual wastage-rate assumed by Dawson and Graves is lower than the investigations of Pettit [15] and Ward [16] show. How the increase in the number of Ayrshire registrations was achieved remains therefore to be investigated. Preliminary results indicate that it was not brought about by keeping cows to a greater age than formerly. Calving for the first time at an earlier age and a reduced calving interval appear to have played some part. It seems probable that there cannot have been much scope for culling of low producers.

It was shown earlier that the geographic distribution of the pedigree Ayrshire population in Great Britain has considerably widened, and that almost twice as many Ayrshire females were in 1946 registered in England, Wales, and Ireland than in their native area—the county of Ayr. This raises the possibility of geographical isolation of breeding groups and the development of local breed-types differing in gene-frequencies from the population as a whole, although this in turn will depend on the effective size of the local population, provided isolation is genetic. Wright [17, 18] has pointed out that, under certain conditions, local differentiation presents more favourable conditions for an effective process of selection and for adaptive advance of the population than is possible under purely panmictic conditions. Breed structure and movement of breeding stock bearing on this problem will be discussed in future papers, but the information already to hand (Table 4) shows that there can be little genetic isolation of regions in the registered Ayrshire population, when (*a*) more than half the sires of registered males come from Ayrshire itself, and (*b*) all regions except Ayrshire and the south-west of Scotland register considerably more males and females than could

be the offspring of bulls bred in the same region—assuming, on average, the same number of offspring per bull, whatever his region of origin. This does not, of course, preclude the possibility of genetic isolation of individual herds within regions. Within the limitation of size of most herds, however, differentiation is more likely to be non-adaptive due to random drift in gene-frequencies than in larger isolated units where selection has a better chance of being effective.

Widening geographic distribution of the Ayrshire breed has also brought it into closer proximity with an increased number of animals of other breeds, thus widening the opportunities for cross-breeding. The bull-licensing figures in Table 5 show that although Ayrshires have become increasingly important as a competitor to other dairy breeds in England and Wales (there has been no increase in the total number of bulls of all breeds licensed between 1936 and 1948), the other dairy breeds are not as yet of any great numerical importance in Scotland relative to the Ayrshire.

TABLE 5. *Bulls Licensed in Great Britain for Five Breeds of Cattle*

*Country and year**	*Ayrshires*	*British Friesians*	*Guernseys*	*Jerseys*	*Shorthorns†*
England and Wales					
1936–7	445	2,502	1,882	613	24,600
1942–3	1,101	9,096	1,111	527	21,268
1948–9	3,154	9,099	1,567	909	11,287
Scotland					
1936	3,877	274	12	21	–
1942	3,930	274	6	12	64
1948	5,713	389	11	28	54

* Licensing years in Scotland run from January 1 to December 31; for England and Wales from March 31 to March 31 of the following year.

† Shorthorns: Figures for Scotland are for Dairy Shorthorns only; for England and Wales all Shorthorns are included: the 11,287 licences issued in 1948–9 consisted of 197 Beef, 3,169 Dairy, and 7,921 General Licences.

Increased opportunities for cross-breeding may imply that genes from other breeds may enter the Ayrshire breed by the process of grading-up to a greater extent than in former times, when the foundation stock in a grading-up scheme was more likely to be non-registered Ayrshires. It may also imply the use of bulls of other breeds on Ayrshire cows with the intention of steering the male calves. Data have, however, not been collected to ascertain the extent of, or the result of, a considered policy of cross-breeding with Ayrshire cattle.

Translated into more practical terms the concomitants of breed expansion of interest to the geneticist are of importance to the breeder also. It poses the questions whether another breed is in fact required in districts where it was not previously found; whether in fact the rate of increase is desirable; whether a breed-structure evolved for a localized breed is a good basis for a breed with a greatly widened distribution.

Summary

The Ayrshire breed of cattle developed in the Cunningham district of Ayrshire in the latter part of the eighteenth and early nineteenth century. It spread, slowly at first, to the surrounding counties, and large-scale movement of the breed into England is of at most twenty years' duration.

Between 1879 and 1946 the number of herds of registered Ayrshire females increased from 51 to 1,948, and the number of females registered from 170 to 24,670. The rate of increase in numbers is roughly exponential when judged by a line fitted by eye. Although the rate of increase of the pedigree Ayrshire population has not been the same in all regions of Great Britain, that stage in an S-shaped growth-curve (to which population growth may be likened) where the rate of expansion begins to decline, had not been reached in 1946 in any of the regions considered in this study; this despite a doubling in the number of female registrations within a five-year period (1943–7).

Up to 1943, the average number of females registered per herd increased in all regions, but between 1943 and 1946 the number of herds increased at a greater rate than the number of females, with a consequent drop in the average number of females registered per herd. It is shown, however, that this drop, which is proportionately much greater in England than in any region in Scotland, is due primarily to the establishment of a relatively large number of new herds which are smaller than their older contemporaries. Also, since 1927, the number of females registered per herd has increased in herds registering more than ten females per herd, but it has decreased in those registering less.

Bull-breeding is still carried on to a greater degree in the native area of the breed than in other regions where Ayrshires are registered. Thus, while 18 per cent. of all females in 1946 were registered by herds in the county of Ayr, 24 per cent. of the males were registered by herds in Ayrshire, and 42 per cent. of a sample of females and 53 per cent. of all the males registered in 1946 had sires bred in Ayrshire.

Some of the genetic implications of pedigree-Ayrshire breed-expansion are discussed.

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BREED STRUCTURE IN THE PEDIGREE AYRSHIRE CATTLE POPULATION IN GREAT BRITAIN

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(With Two Text-figures)

A recent paper (Donald, Deas & Wilson, 1952) reports on the occurrence of an autosomal recessive gene giving rise to dropsical calves in the Ayrshire breed of cattle. It is shown that the occurrence of dropsy, although widespread in the breed, is more common in pedigree herds and that most cases can be traced to bulls bred in a few herds. Moreover, the condition appears to have reached its present wide distribution in less than three decades. As shown in this example, some herds are more significant in the breed than others, but such importance is not of course confined to the spread of deleterious genes. Animals and herds may become significant in breed history because they are thought to be, or are in fact, the bearers of very desirable genes. Robertson & Asker (1951) have shown that the genetic superiority of the 'top' herds in the Friesian breed is ~~about~~ probably less than 100 gal. of milk above that of the 'bottom' pedigree herds, and that the sale of bulls from the 'top' is continually tending to reduce the gap between the two extremes. These facts serve as a practical demonstration of the way in which a few animals or herds assume an importance in the breed as a whole out of all proportion to their numbers.

It can be surmised from what has been written, among others by Lush (1945, 1946), that some form of 'functional stratification' of pure-bred herds exists in most breeds of domestic livestock which are organized into breed societies, exhibited at shows, etc. A rough division for cattle may be made into 'breeders' herds' which supply most of the bulls to other pedigree herds, and 'multipliers' herds' which supply bulls to the 'lower strata' of the breed. The theoretical implications of this are summarized by Lush, who states that 'the reduction in effective size of the population which such stratification causes, will largely increase the chance changes in gene frequency instead of the systematic changes caused by selection, although there will be some of the latter to the extent that stratification is based on the apparent merit of the animals in the herds'.

The primary purpose of this paper will be to show by the use of herd-book data the extent of specialization of function in the Ayrshire breed; an attempt will also be made to deduce some of its effects.

MATERIAL AND METHODS

One of the easiest ways to demonstrate the existence of functional stratification of herds in the breed is to follow back the pedigrees of a sample of registered animals and find out in which herds ancestors have been bred. Accordingly, the first female entry on every sixth page of volume 71 (1947) of the *Ayrshire Cattle Herd Book* was taken until 100 females from Scottish herds had been obtained. Their pedigrees were traced back in full for four generations.

Then, in order to demonstrate possible changes in breed organization over a couple of decades, the data in the herd books for 1927 (volume 50) and 1946 (volume 69) were abstracted, taking all the registered males, and every female on every fifth page of volume 50 (about 11 entries per page) and every female on every tenth page of volume 69 (about 23 entries per page). Herds were then divided into three main groups: (i) those registering males as well as females; (ii) those registering females only; (iii) those registering the occasional male and no females; this last group is small and usually contains small herds or ones recently dispersed. A further classification is used which to some extent cuts across the division of herds made above. Here the fate of the animals bred is the criterion. Herds that breed bulls which have subsequently been used by other pedigree breeders will be called 'breeders' herds', and when not so used 'multipliers' herds' (Lush, 1946). When bulls from breeders' herds have become the sires of pedigree males in other herds, the breeders' herd will be given the suffix (*a*) (thus: breeders' herd (*a*)), when the pedigree offspring of the bulls is confined to females, the breeders' herd will get the suffix (*b*). Multipliers' herds will be given the suffix (i) or (ii), according to the type of registration made in the particular year—as shown earlier.

PEDIGREE ANALYSIS

The pedigrees of the 100 registered females taken four generations back were examined, i.e. a total of 1500 males and the same number of females. Two steps were taken to classify the herds represented in these pedigrees:

(1) Because fewer herds breed bulls than breed

cows, only herds represented by males in these pedigrees were considered; they totalled 244.

(2) The occurrence of a herd in one generation was given twice the weight of an occurrence in the succeeding generation (parent = 2 grandparents = 4 great-grandparents = 8 great-great-grandparents).

The result is not an estimate of the genetic contribution of each herd to the sample animals because in many cases the appearance of a herd later in the pedigree is the direct result of its earlier occurrence in the same pedigree. The method adopted for weighting each herd's contribution, however, gives each generation separately the same weight as if one sought the genetic contribution of that generation to the animals under consideration. Eight of the 244 herds referred to above stood out from amongst the rest for the large size of their contribution to the pedigrees of the 100 females. The same eight herds would emerge if only sires of males were used in selecting them, and, incidentally, only one of the eight herds would not be represented if total number of appearances (not weighted for generation) were the criterion of selection. Since the last mentioned is the simplest classification and gives the same general picture as other methods, it is the one used in Table 1. Two herds—representing less

Table 1. *Distribution of* 244 *herds supplying the males in the four generation pedigrees of* 100 *Ayrshire females from Scottish herds*

Total no. of appearances per herd	No. of herds	No. of males
1	98	98
2–4	79	203
5–9	34	223
10–19	19	259
20–39	6	166
40–59	6	276
60–99	—	—
More than 100	2	275
Total	244	1500

than 1% of the total—are seen to have provided nearly one-fifth of the total bulls in these pedigrees, while at the other end of the scale 40% of all the herds made only one appearance each.

As mentioned earlier, total number of appearances may be misleading and does not indicate the genetic contribution to the sample since the occurrence of an animal from a particular herd may be the result of the occurrence previously of an animal from the same herd or group of herds (for convenience, the sample animals are considered as the starting-point and each generation of ancestors as following later in the pedigree). Fig. 1 shows two sets of numbers: one set shows at each point in the pedigrees of the females the total number of occurrences of bulls and cows supplied by the eight herds combined; the second set (in brackets) shows those appearances of the eight herds which are independent of a previous occurrence of an animal of these herds. Thus, in the parental generation, eighteen of the bulls were bred by the eight herds in question, leaving for further consideration eighty-two out of the initial total of 100 lines of the pedigrees. From amongst the eighty-two bulls which did not belong to one of the selected herds, twenty-nine had sires bred by one of the eight breeders, and so on. The figures in brackets when averaged for each generation add up to give the total genetic contribution from the eight herds over four generations to the sample of 100 females.

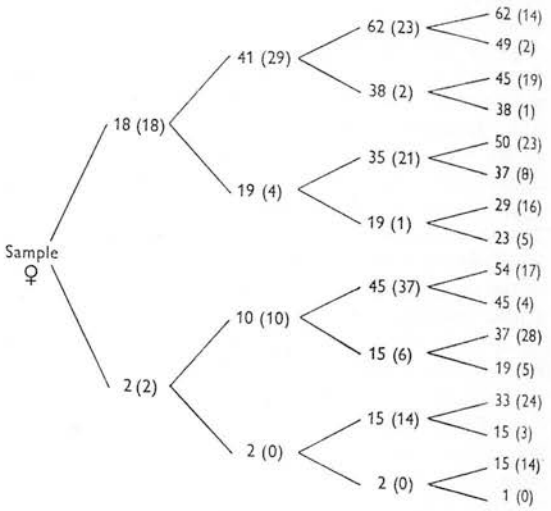

Fig. 1. Occurrence of eight herds in the pedigrees of 100 Ayrshire females registered by Scottish herds in 1947. (The upper arm of each arrow leads to the male ancestor, the lower arm to the female.) (*a*) At each point, the first figure indicates the total percentage contribution of sires (or dams) originating from the eight herds. (*b*) The figure in brackets at each point in the chart shows the number of occurrences of bulls or cows from the eight herds which are independent of appearances of animals from these herds earlier in the pedigree.

It may be seen from Fig. 1 that the total occurrences of males number about twice the total for females. Comparison of the two sets of data shows, however, that most of the females occur because they are the dams of bulls bred in the eight herds. The genetic contribution of the males to the sample is over 40% and of the females less than 5%. Table 2 shows the genetic influence of the two largest contributors, both individually and combined, and of the eight herds treated as a single unit. It will be appreciated that the genetic contribution of herds A and B combined is not the same as the sum

Table 2. *Percentage genetic contribution of eight herds to the pedigrees of* 100 *Ayrshire females*

Herd(s)	Total genetic contribution (%)	Generation 1 Males	1 Females	2 Males	2 Females	3 Males	3 Females	4 Males	4 Females
A	14·7	3·5	0·5	2·5	0	4·1	0·1	3·9	0·1
B	11·0	1·0	0·5	2·5	0·3	3·4	0·2	2·6	0·5
A+B	24·1	4·5	1·0	5·0	0·3	7·4	0·1	5·3	0·5
Eight herds	45·2	9·0	1·0	9·8	1·0	11·9	1·1	9·7	1·7

Table 3. *Genetic contribution of eight herds to contemporary males and females*

	Percentage contribution of genes from eight herds: Parents	Grand-parents	Great-grand-parents	Total for three generations
82 males	20·1	14·4	13·4	47·9
98 females	5·1	14·6	12·1	31·7

of A's and B's individual scores, since to some extent the bulls of one are used by the other. For that reason the total genetic contribution of the eight herds combined does not equal the sum of their individual contributions. A little more than 10% of genes in the sample have come from the eight bull breeding herds for each of the generations that the pedigrees have been followed back. It cannot be argued from this that after nine or ten generations all genes would be attributable to these pedigrees of the males and of the females comes, as seen in Table 3, in the parental generation. Males born are more likely to be registered if they are the sons of bulls from certain herds; conversely, the bulls from these herds leave a larger proportion of male than of female progeny. From Table 3 it follows that whatever genetic contribution some fashionable herds may make to the pedigrees of a sample of females, it is likely that they will make about one generation's contribution more to a contemporary sample of males—provided of course that the influence of the fashionable herds has remained reasonably steady over a few generations.

BREED ORGANIZATION

In the last section it was demonstrated that herds vary considerably in their genetic influence on the breed as a whole. Pedigree analysis is, however, laborious, and it is desirable, therefore, to attempt to classify herds in any particular herd-book year

Table 4. *Herds making registrations in volume* 69 (1946)

Type of herd	Types of registration	Herds No.	Herds %	% of ♂♂ registered	% of ♀♀ registered	No. of ♂♂ registered per herd	No. of ♀♀ registered per herd	Ratio ♀♀/♂♂
Breeders' herds (*a*)	♂♂ and ♀♀	352*	16·7	51·4	32·0	6·9	22·4	3·24
Breeders' herds (*b*) / Multipliers' herds (i)	♂♂ and ♀♀	792	37·4	42·3	40·1	2·5	12·5	4·93
Multipliers' herds (ii)	♀♀ only	807†	38·2	—	27·9	—	8·5	—
Other herds	♂♂ only	162	7·7	6·3	—	1·8	—	—
Totals and averages		2113	100·0	4737	24,670	2·2	11·7	5·21

* Including three herds not registering females.
† Including thirty-one breeders' herds (*a*) but not registering males in 1946.

leading bull breeders, since the importance of individual herds waxes and wanes. It is probable, however, that, as each of the eight herds has been extant for considerably longer than four generations, more than half the genes in the female population of the breed has come through these eight herds—representing rather less than half of 1% of all pedigree Ayrshire breeders. The sires and dams of the 100 sample females in Fig. 1 may also be looked upon as a random sample of eighty-two registered males and ninety-eight registered females (not belonging to one or other of the eight selected herds). It is then found that the percentage contribution of genes from the herds in question was as shown in Table 3. The main differences between the in such a way that their appearances in that year will reflect their genetic influence. To this end the number and type of registrations made by each herd and whether or not animals previously registered by each herd have become sires and dams of the current generation must be taken into account. Study of the registration habits of herds considered in the last section leads to the classification of 1946 herd-book entries shown in Tables 4 and 5. The terminology is that explained under 'Material and methods'. It is self-evident that registration habits could be the same for breeders' and for multipliers' herds, and that some overlap must occur in all but the most complicated classifications. The breeders' herds (*a*) in Table 4 may be subdivided according

to number of bulls registered; the result is shown in Table 5. It must be repeated that the 244 herds whose males were represented in the pedigrees of the last section are, by definition, breeders' herds (*a*) shown in Table 4 and detailed in Table 5. Most of the herds making the largest number of appearances in the pedigrees and shown in Table 1 are represented amongst the thirty herds making most male registrations per herd in Table 5. Some allowance must of course be made for year-to-year fluctuations in numbers registered and for the fact that herds significant some years ago, and thus represented in extended pedigrees, may have been dispersed or become less fashionable by 1946—the year to which the last two tables refer. With these limitations in mind, the classification of herds shows up differences in registration habit certainly between the extremes of the hierarchy—at one end breeders' herds (*a*) whose bulls have been used by other pedigree breeders to breed bulls, at the other, multipliers' herds (ii) many of which are pedigree herds only in the sense that some females have been registered.

On further analysis (Table 5) the significance of a few herds becomes even more apparent; thus, 4 % of all herds are seen to have entered in the herd book of 28 % of all males. Attention must be drawn to the ratio of females/males registered because it is a direct measure of the selection of dams of bulls practised in these herds. The figures show that there can be very little of this in the 'top' herds where 1 male was registered to every 1·3 females, while in the population as a whole the ratio was 1:5·2 (Table 4). Implications of this will be discussed later.

The difficulty engendered by allotting herds to any one stratum when function in one year conflicts with that in a later year, makes it apparent that the position of any particular herd in any 'stratum' of breed organization is mainly a position in time. The position of a herd at any particular moment of time depends on the personal characteristics of the breeder—whether he is able (or prepared) to turn his herd into a 'breeders' herd'. It must also depend on the willingness of other breeders to recognize and encourage the pre-eminence (whatever its

Table 5. *Classification of breeders' herds* (*a*)*—by numbers of bulls registered* (*from volume* 69, 1946)

Male registrations per herd	No. of herds	% of herds	% of all ♂♂ registered	% of all ♀♀ registered	No. of ♂♂ registered per herd	No. of ♀♀ registered per herd	Ratio ♀♀/♂♂
20	15	0·7	9·0	2·3	28·3	37·8	1·33
15–19	15	0·7	5·2	2·0	16·4	32·3	1·97
10–14	56	2·7	13·8	6·0	11·7	26·4	2·25
5–9	112	5·3	16·2	11·4	6·8	25·1	3·67
1–4	154	7·3	7·2	10·3	2·2	16·6	7·34
Totals and averages	352	16·7	51·4	32·0	6·9	22·4	3·24

The results (Table 4) obtained from analysing the registrations of these 'types of herds' are not unexpected. Breeders' herds (*a*) can be assumed to be better established in the pedigree market than other groups and can therefore be expected to register most males per herd. This is confirmed in Table 4, which also shows these herds to register most females per herd. At the other end, multipliers' herds (ii)—38·2 % of all herds in 1946—are the smallest herds in terms of females registered per herd (8·5). Herds registering both males and females but whose bulls become sires of non-pedigree stock, or of pedigree females only, are intermediate. The small class of herds registering males only in 1946 has been referred to earlier and is not considered significant.

These data are presented to emphasize that a relatively small proportion of the herds (16·7 %) registered more than half the males (51·4 %) and a third of the females in the herd book. On account of this and because of the use made of the bulls they breed, these are the significant herds in the breed. basis) of one of their number. 'Stratification' of herds in the Ayrshire breed should not, therefore, be visualized as a hard and fast division, but rather as several functional stages within the one population. Graphical illustration makes this continuity within the population easier to visualize. Fig. 2 was drawn by using the data in Tables 4 and 5. The horizontal axis shows the cumulative percentage of all pedigree herds in 1946 starting with the largest fifteen herds (0·7 %, Table 5) at the top. The groups in Table 5 registering 1–4 and 5–9 males per herd have been combined. The percentage of herds is divided equally on either side of a central vertical axis showing the cumulative percentage of all males registered. The upper part of the figure (above the upper horizontal line) comprises breeders' herds (*a*). The next major division (between the horizontal lines) comprises breeders' herds (*b*) registering males and females in 1946, multipliers' herds (i) and the small group of herds which registered males only in 1946. Herds below the lower horizontal line are the large group (38·2 % of all pedigree herds in 1946)

of multipliers' herds (ii), i.e. those registering females only, although here also a number of breeders' herds is found.

In order not to draw artificial divisions between the various 'groups of herds', the breed structure could be visualized as three-dimensional—a conicoid figure which would be generated by a concave line (see Fig. 2) about a fixed point (the apex of Fig. 2). As herds move upwards from the base, the number of bulls produced and their influence on the breed would be in an inverse ratio to the number of herds breeding them. A few bulls may move upward in the structure, but the general trend of movement of bulls at any point is visualized as downward. Functional stratification thus becomes merely convenient terminology for indeterminate phases of dynamic breed structure represented by a conicoid figure.

COMPARISONS BETWEEN 1927 AND 1946

If registration habits are correlated with herd function, then changes in registration habits should reflect changes in the breed hierarchy. It has been shown by Wiener & Yao (1952) that both in 1927 and 1946 some 40 % of all farmers making entries in the Ayrshire herd book registered only females. For the present comparison, therefore, only herds where males are also registered will be considered. Table 6 presents registration features of these herds.

The most noteworthy feature of Table 6 is that the increase which took place between 1927 and 1946 in the number of herds registering males was far larger than that in breeders' herds (*a*). Consequently, while breeders selling bulls to non-pedigree herds and for breeding pedigree females increased sixfold in number, breeders' herds (*a*)

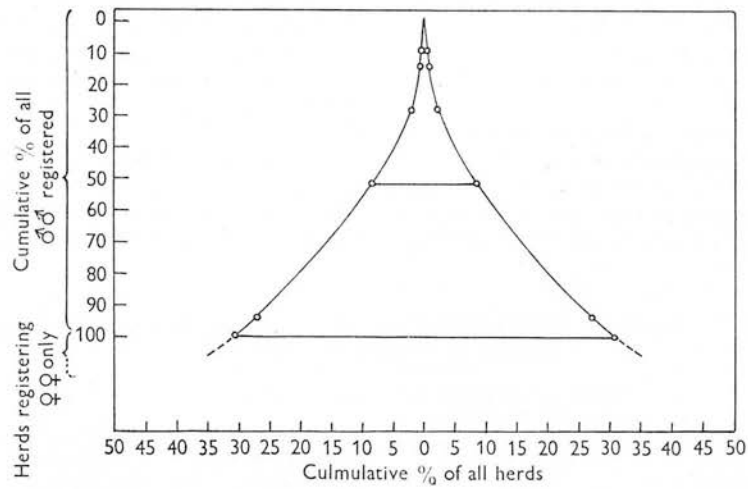

Fig. 2. Diagram of pedigree Ayrshire breed structure. Herds are arranged according to the number of males registered per herd, and according to whether they are breeders' or multipliers' herds (see text).

Table 6. *Features of bull registrations from breeders' herds* (*a*) *and other herds registering males*

Herd-book year ...	1927	1946	Changes 1927–46 1927 = 1
No. of herds registering ♂♂	290	1314	4·5
No. of breeders' herds (*a*)	152	412	2·7
Breeders' herds (*a*) registering ♂♂ in the same volume of the herd book:			
No. of herds	129	352	2·7
Average no. of ♂♂ registered per herd	4·23	6·92	1·6
*Herds registering ♂♂ except breeders' herds (*a*):			
No. of herds	161	962	6·0
Average no. of ♂♂ registered per herd	1·75	2·39	1·4

* These herds were in the last section classified as breeders' herds (*b*) and multipliers' herds (i).

increased by less than half that amount (2·7). However, the absolute increase in numbers of breeders' herds (*a*) from 152 to 412 may be of greater moment in terms of the effective size (*N*) of the population than the decrease in the relative proportion of this group. This will be discussed later. The number of males registered per herd increased about equally in all classes (1·6 times in breeders' herds (*a*), 1·4 times in other herds), and it seems therefore that this increase is merely the result of breed expansion, that is to say the larger demand for pedigree Ayrshire bulls in 1946 as compared with 1927.

Breeders' herds (*a*) differ in importance according to the number of offspring the bulls they breed leave in the population as a whole. This number depends both on their bull output and on the extent to which individual bulls are used. Both of these factors may be combined by taking the total number of registrations in any herd book which are the progeny of all bulls bred in each herd and represented in that year. Thus, two herds would rank of equal importance if each could be attributed with ten registrations—although in one case these may be the progeny of a single bull bred in one herd, while in the other case ten may be the offspring of ten different bulls bred in one herd. This is the method employed in subdividing breeders' herds (*a*) in Table 7. It shows the numbers of all males registered in the 1927 and 1946 herd books which are the offspring of bulls bred by single herds; it shows the specialization of function to which this has led.

The first point about Table 7 is that it shows how only a small proportion of all herds is significant in the breed. This conclusion was also drawn from Tables 4 and 5, only then the basis of classification was the number of males registered by breeders' herds, now the evidence is more direct in that it shows the number of offspring of bulls from breeders' herds. The next point of Table 7 is that the proportion of herds significant in 1946 is smaller than that in 1927; accordingly, the individual significance of some herds in 1946 is greater than the importance of the equivalent herds in 1927 (compare 2·6 % of herds breeding the sires of 22·9 % of the registered males in 1927 with 1·5 % of herds and 25·8 % of males respectively in 1946, etc.).

It can be shown, moreover, that bulls from herds at the top of the hierarchy are used longer than bulls from herds lower down. Thus, a sample of females registered in 1946 was analysed in a similar way to the males in Table 7. Herds which had supplied bulls as sires of these females were grouped according to the total number of bulls supplied per herd. A total of 249 herds were represented by 648 bulls which had sired the sample of 2231 females. 4·8 % of the herds were represented by more than ten bulls each (27·1 % of all bulls); the average age of these bulls at the birth of their female progeny was 4 years 2·2 months. At the other end of the scale nearly half of the 249 herds were represented by only one bull each and their average age at birth of offspring was 3 years 5·9 months. One of the most likely explanations for this is that big herds using more than one bull can employ each over a longer period of time and still avoid mating him to his daughters; these herds are

Table 7. *Breeders' herds (a) grouped according to the number of registered male progeny of the bulls they have bred*

Herd-book year	Number of registered ♂ progeny of all bulls originating from any one breeders' herd (*a*)	Percentage of all breeders' herds (*a*)	Percentage of all ♂♂ registered
1927	>30	2·6	22·9
	20–29	4·6	19·4
	10–19	8·6	19·0
	5–9	11·2	13·8
	2–4	36·2	18·1
	1	36·8	6·8
	Total no.	152	828
1946	>100	1·5	25·8
	50–99	2·2	15·4
	30–49	5·8	19·4
	15–29	7·8	12·9
	10–14	7·0	7·6
	5–9	16·3	9·4
	2–4	29·8	6·9
	1	29·6	2·6
	Total no.	412	4737

also likely to be the ones that can afford to purchase bulls from breeders' herds at the top of the hierarchy.

Between 1927 and 1946 there has been a large increase in numbers of all pedigree herds and a proportionately smaller, but nevertheless noteworthy, growth in the group of breeders' herds. These data do not directly answer the question whether or not there has been an equivalent rise in the genetically effective size of the breeding population. The indications are that there has not. The very small number of herds (perhaps eight or ten) which are the 'ultimate' suppliers of bulls seem to have remained constant. There has, however, been an increase between 1927 and 1946 in specialization of herd function inasmuch as a wider 'gap' must now be traversed by breeders moving from one end of the hierarchy to the other.

DISCUSSION

The specialization of herd function in the Ayrshire breed of cattle demonstrated in this paper has at least two consequences of particular interest to the geneticist and animal breeder.

The first of these is that it creates a bottleneck through which most of the genes of future generations must pass. Taking a long-term view of Wright's (1931, 1940) concept of the effective size (N) of the population, this will be determined more by the size of the 'bottleneck' than by the potential number of parents in any one generation. Evidence offered earlier showed that rather more than half the genes in the pedigree population came from eight herds. Examination of the 1000 males registered by these eight herds in a 6-year period 1943, volume 66, to 1947, volume 71, showed them to have been sired by some 100 bulls, but as nearly half of these left only one or two offspring each, about fifty or sixty bulls sired most of the male registrations. About 15 % of these registrations in the earlier half of this 6-year period and nearly one-quarter in the latter half are progeny of fourteen bulls not bred in these herds. The pedigrees of these fourteen bulls show, however, that all but one are sons or grandsons of bulls from the eight herds. Incidentally, in six of the eight herds the percentage of bulls used but not bred by them averaged less than 10 %. It appears then that roughly eight new bulls become effective in these eight herds every year or approximately thirty-two per generation, taking one generation as 4 years. The effective number of males (Nm) per generation in the population as a whole would be not quite twice the thirty-two due to these herds (since only something over half the genes come from the eight herds.) Such an estimate of Nm would fall within the range given by Lush (1946) for several breeds of cattle. The loss of heterozygosis under random mating ($1/[8Nm]$, Wright, 1931) resulting from this number would be only about 0·2 % per generation. In practice, the situation is complicated by the fact that more than half the males registered in the eight herds are sons of bulls from two of them, and these two have used extensively about twenty bulls over the 6 years studied, three-quarters of them of their own breeding. For 1927, when Fowler (1932) estimated inbreeding in the Ayrshire breed at 0·5 % per generation, the resulting estimate of Nm would be 25. For comparison, it is interesting to note that in British Friesian cattle, Robertson & Asker (1951) estimated the top group to consist of some 20–30 herds, and one of them of outstanding importance.

A second consequence of the breed structure is the effect it has on selection for milk yield. That the herds selling many bulls to pedigree breeders do in fact have higher herd averages for milk yield than average for the breed may be seen from published milk records. But the genetic portion of the difference between their yield and breed average is not known. As mentioned in the introduction, Robertson & Asker (1951) estimated that for Friesians the genetic superiority of the top herds is ~~about~~ probably less than 100 gal. of milk above the bottom pedigree herds.

In a rapidly expanding population like the Ayrshire breed at present, as many of the females born as can be reared are likely to enter the breeding population (Wiener & Yao, 1952). Any genetic improvement to be expected must thus come through the bulls, either progeny tested, or selected on the records of their dams, relatives, or both. The efficiency of the progeny test method will depend, as discussed by Robertson & Rendel (1950), on the size of the unit. It may be of no advantage they point out in a unit of 120 cows, since the increase in the generation interval offsets the advantage of extra information about a sire's genotype, but it would give an increased rate of genetic improvement over other methods of selection in a unit of 2000 cows. Until such time as artificial insemination or co-operative methods substantially increase the size of breeding units in Ayrshire cattle, the most usual method of selection for production is likely to remain selection of dams of bulls.

Mahadevan (1951) has estimated the genetic superiority of dams of bulls sold by twelve well-known Ayrshire herds as 35 gal. Only three of the herds he chose were amongst the first twenty herds in 1927 and in 1946, as judged in this paper by the number of male offspring sired by their bulls. In these three herds, the estimated genetic superiority of the dams of bulls sold is considerably below the average for all twelve herds. This is easily understood when it is noted that over the period considered by Mahadevan, 80 % of the estimated number of males born in these herds were registered,

and, by implication, available for sale; in the other nine herds, the proportion of male registrations was lower. In two of the three herds, the dams of bulls retained in the herds are estimated as genetically superior to the dams of bulls sold.

As an alternative to using most of the bulls bred by a few herds, as at present, one might take say 20 % of the best dams in every herd and breed bulls from these. The genetic superiority (Ig) of these dams could be expected to be: $Ig = \bar{\imath} h^2 \sigma_p$ (Rendel & Robertson, 1950), where $\bar{\imath}$ is the superiority in terms of standard deviation, and would be 1·4 in this case (Lush, 1945: p. 148), h^2 the heritability of milk yield, assumed at 0·25, and σ_p the phenotypic standard deviation in yield. σ_p for milk yield was estimated by Rendel & Robertson to be $0{\cdot}20\bar{Y}$, where $\bar{Y}$ is the average herd yield. If this is taken to be 600 gal., it would result in an estimated superiority of cows to breed bulls of 42 gal. of milk —a figure to be compared with Mahadevan's 35 gal. for dams of bulls bred in the 'top' herds. Depending on the validity of the assumptions made, the genetic effect of choosing dams of bulls in the two ways discussed does not appear to differ much.

SUMMARY

Ayrshire Cattle Herd Books for the years 1927, 1946 and 1947 were examined to study the breed structure. Extended pedigrees of a sample of registered females showed that more than half their genes had come from eight herds. Most of the genetic contribution of these herds comes through the bulls they breed.

Herds were divided into: breeders' herds (*a*), breeders' herds (*b*), multipliers' herds (i), multipliers' herds (ii), and herds registering males only. The function and numerical importance of each group is shown. The position of any one herd in the breed hierarchy is unstable. Changes in the extent of specialization of herd function between 1927 and 1946 are described.

The Ayrshire breed structure is discussed in the light of its implications on the effective size (N) of the population and on the selection of bulls for breeding.

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MIGRATION OF PEDIGREE AYRSHIRE CATTLE IN GREAT BRITAIN

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Pedigrees of animals from the principal cattle breeds show that a majority of calves born in any herd have sires purchased from other herds, and that many calves also have dams which were not home-bred. In this paper an attempt will be made to assess the amount of movement of pedigree animals within the Ayrshire cattle population in Great Britain and to discuss the reasons and consequences.

Migration is a direct consequence of the geographical distribution of leading herds and of breed stratification, whereby a comparatively few herds dominate the production of males for breeding. For Ayrshires, the south-west of Scotland constitutes a centre of radiation of the breed (Wiener & Yao, 1952). Population dynamics have been described for a number of breeds of cattle, pigs, and sheep, and the following may be cited: cattle—Donald (1945), Robertson & Asker (1951), Wiener (1953), Wiener & Yao (1952), Stonaker (1943), Young (1953), Stewart (1952); pigs—Donald (1940); sheep—Stevens (1948), Wiener (1954). Direct measures of movement for various breeds are given by Engeler (1943), Robertson & Asker (1949), and Stewart (1952). These papers show that the same features occur in Switzerland, Great Britain and New Zealand.

MATERIAL AND METHODS

The material for this study consists of random samples of 951 females registered in vol. 50 (1927) of the *Ayrshire Cattle Herd-Book*, 1946 females from vol. 69 (1946) and 1020 males from vol. 69. The herd-book appendices were not sampled. Check samples of approximately the same size gave similar results and will not be quoted; they could not be combined with the data shown because of an overlap in the two samples taken for each year. Registration procedure was the same in 1927 and 1946. For every animal in the sample, the following information was noted: (*a*) county of owner; (*b*) county of mating breeder, where different from (*a*); (*c*) county from which sire of sample animal was registered; (*d*) county from which dam of sample animal was registered.

Great Britain and Ireland have been divided into regions which in a previous study (Wiener & Yao, 1952) were found to correspond roughly to centres of breed distribution. The name given to each region is broadly descriptive of its location in the British Isles except that 'south-west Scotland' excludes the county of Ayr—the latter is classed separately.

RESULTS

In 1946 more than a third of the females and more than two-fifths of the males in the herd-book had been registered by breeders in England and Wales, but these proportions do not apply to the parental generation. Many of the bulls and cows bred from in England had come from Scotland. But in addition to the north to south traffic in stock, a considerable amount of transference took place between and within the regions of England, Wales and Scotland. In consequence, few of the animals registered by farmers in any region had parents also registered from the same region. Even fewer animals registered from any one herd had both sire and dam home-bred. The situation is summarized in Table 1. The numbers refer to females and males bred in and registered from the same region (or herd), and the percentages refer to the proportion of these animals which had both parents registered from the same region (or herd).

Three-quarters of both males and females registered from Ayrshire had both parents registered from Ayrshire, but in all other regions this proportion was appreciably lower—about half from Ireland, about one-third from south-west Scotland and between 0 and 23 % elsewhere. More home-bred animals became the parents of females than of males. The emphasis on purchased sires and dams noted within regions is even more apparent within herds. The highest proportion of calves born to two home-bred parents was in herds in Ayrshire, and even there less than 20 % for females and only 14·6 % for males. With the single exception of female registrations in south-west Scotland, all other values for the proportion of calves born to two home-bred parents within herds is less than 8 %.

Some of the movement which results in the situation represented by Table 1 took place in the period between the mating of sire and dam and the registration of the resulting progeny. In the county of Ayr, for example, the number of females produced

as a result of matings in Ayrshire exceeded the number registered (363) by breeders in Ayrshire during 1946 by nearly 6 %. These 6 % were registered in herds elsewhere and presumably exported *in utero* or as young calves before registration. Conversely, from England, registrations exceeded the number resulting from matings in England by about 10 %. In 'south-west Scotland' conceptions also exceeded registrations; but from the 'rest of Scotland', as from England, registrations exceeded matings. More males than females were transferred in this way. The actual numbers may be got by difference between the numbers registered shown in Table 1, and the numbers bred in each region as shown in Tables 2 and 3.

Most stock movement, however, took place subsequent to registration and prior to mating, i.e. through the purchase of herd sires and female herd replacements. A majority of bulls in England had come from Scotland (about 55 % sires of ♀♀, and 64 % sires of ♂♂) but very few of the herd sires used in Scotland had originated in England. Transfer of bulls between regions within England accounted for a further 15 % or so of movement. In Scotland, outside Ayrshire, about half the bulls used had come from herds in Ayrshire. From detailed data on inter-region movement there was little suggestion that breeders went to their nearest market for bull or cow replacements. Such importance as any particular region had for exporting animals was due to the existence of a number of prominent herds in that region.

Some of the details for the above generalizations are given in Table 2 for a sample of females and in Table 3 for males. Complications due to migration between conception and registration, referred to above, are excluded from these tables by considering the distribution of the sample animals at the time of mating, i.e. 9 or more months before registration.

Table 2 shows that a greater proportion of cows (col. 2) than of bulls (col. 1) stayed for breeding in the region from where they were registered, also, that there appears to be considerable variation between regions. For example, in Ayrshire, nearly all cows for breeding were natives of Ayrshire, whereas in south-west England less than a third had been reared in that region. Similarly,while 81 % of the bulls used in Ayrshire had as calves been registered from there, the 'region-bred' proportion in south-west England was only 12 %. From Ayrshire itself had come about a third of the sires used in England and an even larger proportion of those used in Scotland. An appreciable number of bulls was also exported from south-west Scotland (col. 4). The proportion of English bulls bred from in Scotland was very small (2·3 % in Ayrshire, 1·4 % in south-west Scotland). The detailed data show that most of the bulls concerned had come from adjoining northern England.

Not unexpectedly, the pattern of movement observed among males (Table 3) is similar to that already noted among females, but an even greater emphasis appears to be placed on parents from Ayrshire itself. Thus, while 30·8 % of females bred in the various regions of England had had sires from the same region, the equivalent proportion among males was 7 % less. Similarly, fewer males than females were registered from region-bred cows in England and the 'rest of Scotland' (cf. cols. 2 of Tables 2 and 3). More than half the males (51·3 %) in the sample of 1020 are offspring of bulls registered from Ayrshire, whereas 47 % of the 1946 females in the sample had sires from Ayrshire. This suggests that in the registration of bulls there is some selection for sires from Ayrshire additional to that practised in the registration of females.

Ireland was the only region outside Ayrshire and the south-west of Scotland to use a majority of home-bred bulls and cows (i.e. 'region-bred' in the terminology of Tables 2 and 3), but even so, some 30 % of the bulls mated in Ireland had been purchased in Scotland.

In the period before the Ayrshire breed greatly expanded into England—that is in the years before 1927—the parents of registered animals stemmed largely from the native region of the breed. A sample of females from the 1927 herd-book confirms this (Table 4).

The amount of migration shown in Table 4 is similar to that shown in the previous two tables, but it may also be seen from a comparison of Tables 2 and 4 that the increase in the population of Ayrshire cattle in England between 1927 and 1946 had not been accompanied by a corresponding increase in the number of bulls bred there.

It was observed in these data that only rarely are local bulls mated to imported cows, but that the converse is a frequent practice. It was also noted that some 10–30 % of the bulls bred are exported from regions which themselves import large numbers. These sales are not confined to neighbouring regions and cannot therefore be attributed merely to the arbitrary divisions between regions. Thus, with the exception of Ayrshire and south-west Scotland, there was in 1946 neither a sufficiency of breeding stock in any area to meet its own demand, nor any attempt to use at home all available local stock.

Because the predominant breeders' herds in the Ayrshire breed in 1946 were concentrated in Ayrshire and the south-west of Scotland, gene frequencies in the breed as a whole will tend to follow those prevailing in the population in Ayrshire and south-west Scotland. Thus, half the genes in a sample of females registered by farmers from England and Wales came from Scotland in one generation, and

Table 1. *The proportion of registered cattle which were conceived in and registered from one region (or herd) and which had both parents registered from the same region (or herd)*

Sample of		Scotland			England						Wales	Ireland
		Ayrshire	South-west	Rest	Northern	West-midland	East-midland	Eastern	South-east	South-west		
♀♀	No. registered	363	661	236	129	111	40	97	176	80	27	26
	Percentage with two parents registered from the same REGION as offspring	75·2	37·2	11·0	19·4	15·3	5·0	20·6	22·7	10·0	3·7	46·2
	Percentage with two parents registered from the same HERD as offspring	18·7	12·9	5·5	6·2	4·5	2·5	7·2	5·7	5·0	0	7·7
♂♂	No. registered	206	265	102	91	96	31	43	78	45	14	49
	Percentage with two parents registered from the same REGION as offspring	74·3	31·3	8·8	11·0	9·4	0	9·3	17·9	6·7	0	51·0
	Percentage with two parents registered from the same HERD as offspring	14·6	6·0	3·9	3·3	0	0	2·3	3·8	2·2	0	2·0

Table 2. *Percentage distribution—by region—of parents of a sample of females registered in vol.* 69 (1946) *of the herd-book*

Region of mating breeder	No. of progeny	Type of mating: Region-bred		Type of mating: Sires from			
		Sire (1)	Dam (2)	Ayrshire (3)	S.W. Scotland (4)	Rest of Scotland (5)	England and Wales (6)
Ayrshire	384	81·0	95·9	81·0	15·7	1·0	2·3
S.W. Scotland	720	57·3	93·3	39·2	57·3	2·1	1·4
Rest of Scotland	220	21·8	80·0	54·1	24·1	21·8	—
England							
Northern	117	29·9	67·5	31·6	35·9	—	32·5
West-midland	94	36·2	47·9	35·1	17·0	2·1	45·8
East-midland	37	13·5	59·5	37·9	18·9	—	43·2
Eastern	95	29·5	64·2	35·8	10·5	3·2	50·5
South-east	166	36·2	66·3	37·3	17·5	—	45·2
South-west	73	27·4	39·7	24·7	17·8	—	57·5
Wales	16	12·4	31·2	12·5	25·0	—	62·5
England and Wales (Regions totalled and averaged)	598	30·8	58·6	33·5	20·2	0·8	45·5
Ireland	24	70·8	62·5	8·4	20·8	—	—

these almost entirely from the two areas mentioned. Sixty per cent of the genes of a sample of males was similarly 'Scottish'. This is shown in Table 5 which takes account of all the components of movement in the cycle of a single generation.

From Table 5 it is seen that the largest source of 'English' genes (cols. 2) for animals registered from England is their dams, while the biggest influx of imported genes (cols. 3) came through sires. Transfers between mating and registration (col. 4) amounted to about 10%. If these populations of registered males and females were the sole parents of the next generation, the latter would still have some 55·1% imported (Scottish) blood—not counting importations in previous generations.

DISCUSSION

The questions recur: what are the reasons for the large amount of migration of Ayrshire cattle within the British Isles noted in this study, and what are the consequences?

A primary reason, already suggested earlier in this paper, is the comparatively small number of bull-breeding herds which supply a scattered market (Wiener, 1953). Moreover, the concentration on a few animals and herds will be further accentuated by the use of artificial insemination. A second reason for migration is expansion in the dairy cow population, as in 1946, with a consequent transfer of females from areas with a surplus to those with a

Table 3. *Percentage distribution—by region—of parents of a sample of males registered in vol.* 69 (1946) *of the herd-book*

		Type of mating					
		Region bred		Sires from			
Region of mating breeder	No. of progeny	Sire (1)	Dam (2)	Ayrshire (3)	S.W. Scotland (4)	Rest of Scotland (5)	England and Wales (6)
Ayrshire	238	79·4	92·8	79·4	16·0	1·3	3·3
S.W. Scotland	295	53·2	93·6	44·1	53·2	—	2·7
Rest of Scotland	92	20·7	76·1	57·6	21·7	20·7	—
England and Wales (Regions totalled and averaged)	348	23·8	43·1	42·2	19·0	1·7	37·1
Ireland	47	70·2	66·0	8·5	19·2	2·1	—

Table 4. *Percentage distribution—by region—of parents of a sample of females registered in vol.* 50 (1927) *of the herd-book*

		Type of mating					
		Region bred		Sires from			
Region of mating breeder	No. of progeny	Sire (1)	Dam (2)	Ayrshire (3)	S.W. Scotland (4)	Rest of Scotland (5)	England and Wales (6)
Ayrshire	276	87·3	93·1	87·3	9·1	3·6	—
S.W. Scotland	567	66·7	96·5	33·0	66·7	0·7	—
Rest of Scotland	53	26·4	64·2	51·0	22·6	26·4	—
England and Wales (Regions totalled and averaged)	53	16·9	39·6	35·9	39·6	—	24·5

Table 5. *Proportion of genes from different sources in samples of Ayrshires registered from England and Wales in* 1946

		Source of genes (%)				
		Region bred		Imported		
Sex of registered animal	Registrations No. in sample (1)	Sires (2)	Dams (2)	Sires (3)	Dams (3)	Transfers between mating and registration (4)
Female	660	20·6	30·1	24·7	15·2	9·4
Male	398	16·2	22·9	27·5	20·8	12·6

deficit. In the same manner, the process of herd attestation is a cause of movement. While these reasons may in part explain the movement of Ayrshires from Scotland to England, they provide a less adequate explanation of the movement between regions in England and Wales and within Scotland. A wish to avoid inbreeding may weigh against the use of a home-bred animal, while advertisement and repute may strengthen the desire for an 'imported' one.

A direct consequence of this movement is that the breed is no better genetically than the bull breeders make it. Since most (Johansson & Robertson, 1952) or all (Robertson & Rendel, 1954) herd differences in milk yield can be assumed due to environment, little genetic advance in yield can be expected from migration. This is not to deny that individual herds may not make such advance, but only to suggest that the average effect appears to be a maintenance of the genetic *status quo*.

The occurrence of frequent outbreaks in recent years of serious cattle diseases (Reports on Animal Health Services, 1953, 1954), and their transmission over often long distances through migration of animals, suggests that from a husbandry point of view these transfers have little to commend them.

SUMMARY

Migration of pedigree Ayrshire cattle in the British Isles is estimated for 1927 and 1946 from samples of herd-book registrations. Most migration is from Scotland, particularly Ayrshire, to England, but considerable numbers were also transferred between regions within Scotland or England. A larger proportion of bulls than of cows was moved in this way. Only a small proportion of animals had two parents bred in the same herd as themselves. If the males and females registered from England in 1946 were the sole parents of the next generation, the latter would still have more than half Scottish blood.

The amount of movement of Ayrshire cattle shown by these data virtually precludes genetic differences between regions, but not perhaps between herds. Other implications of movement are discussed.

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42

THE SIGNIFICANCE OF GRADING-UP IN THE AYRSHIRE CATTLE POPULATION OF GREAT BRITAIN

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The object of the investigation reported here was to discover the extent and effects of grading-up in the Ayrshire cattle population. By 'grading-up' is meant the process whereby the descendants of non-pedigree animals are allowed into the pedigree population. It is not to be confused with any other use of the same term.

The genetic consequences of grading-up will depend on how much grading-up is practised both in individual herds and in the population as a whole, on how different the grading-up animals are from the pedigree animals, and on the amount of selection for or against grading-up ancestry in the choice of breeding stock, particularly bulls.

Animals in the process of being graded-up to pedigree status are registered by the Ayrshire Cattle Herd Book Society in an Appendix to their *Herd Book*. Such an Appendix has been published since 1887, that is, ten years after the *Herd Book* itself was started. Since 1904, this Appendix has been open to females only, and since 1909 has consisted of two sections, B and A. Until 1909 entry into the Appendix, and until 1917 entry into Appendix B was by inspection for type coupled, for some time, to winning a prize in the Ayrshire class at an agricultural show and, later, to reaching a specified milk and fat yield. Since 1917, entry to Appendix B has been confined to daughters of pedigree Ayrshire bulls and has continued to be subject to type and yield requirements. The yield qualifications quoted in the 1952 *Herd Book* are, in respect of heifers, 285 lb. butterfat in a lactation with a calving interval of 13 months, 313 lb. with an interval of 14 months, and 342 lb. with an interval of 15 months. There are similar adjustments for the yield expected from cows qualifying for entry in Appendix B (henceforth called 'B' cows). The average butterfat percentage in a qualifying lactation must not fall below 3·5 %. The daughters of B cows and pedigree Ayrshire bulls are eligible for entry in Appendix A (to be called 'A' cows) and their female offspring, again by a pedigree bull, are eligible for entry in the *Herd Book* with a number. The females at this stage of the grading-up process will be termed 'P_A' cows. Not only the female but also the male progeny of these P_A cows and pedigree bulls may be entered in the pedigree section of the *Herd Book*. All animals registered in the pedigree section of the *Herd Book*, other than P_A females, will be designated 'P'.

MATERIAL AND METHODS

The data on numbers of animals and of herds were obtained from the published volumes of the Ayrshire Cattle Herd Book Society, usually by taking random samples of animals and herds. A detailed analysis of all registrations in the 1946 (vol. 69) *Herd Book* was made because much information about the breed statistics in that year has already been published (Wiener & Yao, 1952; Wiener, 1953). The latest volume available when this part of the work was done (vol. 76, 1951) was sampled to give a more recent estimate of the extent of grading-up. Another sample of 200 females comes from the 1947 (no. 71) volume of the *Herd Book*; part of their pedigrees were originally used in connexion with other investigations (Donald, Deas & Wilson, 1952; Wiener, 1953).

Milk yields for heifers completing their first lactation in Scottish milk-recorded herds in 1955 were made available through the courtesy of Mr G. Haydock of the Livestock Records Bureau. Data were abstracted for all herds which had in milk at least one A or P_A heifer. For all such herds, every contemporary P heifer (as well as every other A and P_A heifer) was noted. The heifers themselves had *Herd Book* numbers placing them in the registration years 1952 and 1953. Three sets of yield comparisons could then be made within herds:

(1) Pedigree daughters of pedigree dams (P) with Appendix A females (A).

(2) Pedigree daughters of Appendix A dams (P_A) with Appendix A females (A).

(3) Pedigree daughters of pedigree dams (P) with pedigree daughters of Appendix A dams (P_A).

Since the P group consists of a mixture of pedigree cows, ranging from daughters of P_A cows to those with no grading-up ancestry since the beginning of the *Herd Book*, the genetic 'step' from P_A to P in the present context differs from the 'step' from A to P_A.

Appendix B females had to be excluded from the analysis of 1955 milk records since their registration takes place after the end of the first lactation, and

was not therefore known at the time these lactation records were received.

Some 10 % of lactation records for the year 1955 had not arrived at the Livestock Records Bureau at the time this investigation was brought to a close. The omission of these records is not thought to affect in any way the contemporary comparisons of yield of heifers in the three *Herd Book* registration classes, nor the conclusions to be drawn. All animals with lactations of less than 100 days were excluded. Yield up to 305 days was used for all lactations in excess of such length.

RESULTS

The extent of grading-up

The history of the registered Ayrshire cattle population may conveniently be divided into five periods of approximately 15 years each. After a formative period lasting until about 1892 the registered numbers kept increasing and reflecting the fortunes of farming and milk production in particular. Thus the period 1907–21 was marked by a five-fold increase over the numbers registered in the previous 15 years, whereas the number registered in the following period of agricultural depression, 1922–36, showed an increase of only 25 % in numbers. Between 1937 and 1952 over half a million Ayrshire females were registered in the *Herd Book* and its Appendix—another five-fold increase over the previous period. The numbers in the Appendix, more or less as expected, were high initially—accounting for 20–30 % of all registrations—then decreased greatly, both absolutely and proportionately, in the 1922–36 period, and increased again enormously during the most recent boom in milk production. The numbers registered in Appendix B were approximately as follows: 8726 (1909–21), 621 (1922–36), 16,697 (1937–52) (these numbers are approximate because they were obtained by subtracting the first from the last registration number of the B Appendix each year, and not all numbers are allocated).

The reduction in the amount of grading-up in the 1922–36 period appears to have been governed by the numbers registered in the Appendix B, and not by any discrimination against the offspring of Appendix cows. This is apparent if the numbers registered in each class over a period of years, are expressed as percentages of the numbers registered in the parental class over a similar period of years. Both the generation interval and the age at registration must be taken into account, since the latter at any rate differs between B, A and pedigree stock. (For example, B animals are registered as adults, P animals as young calves.) The average age of cows at calving was found to have decreased by some 6–9 months over the past 30 years, but 5 years may be taken as an average. Table 1 shows, for four periods, the number in each registration category as a percentage of the number in a preceding period from which it could have been bred; thus, P animals can be bred from P or P_A; P_A animals from A; and A heifers from B cows. Appropriate adjustments have been made for generation interval and age at registration as described.

Table 1. *Number of registered female offspring from 100 female parents in different registration classes*

Period of registration of ♀ offspring	Class of ♀ parents: P+P_A	A	B
	Number of ♀ offspring per 100 ♀ parents		
1892–1906	88	100	—
1907–1921	106	122	109
1922–1936	113	187	314
1937–1952	175	215	219

Slightly different estimates of reproductive rate would have been obtained if different periods of years had been chosen for parents or offspring, but the general trend would not have altered. The figures show that a greater number of female offspring are registered from Appendix than from pedigree cows. For animals born in, for example 1937–52, an inference from the data is that pedigree (P and P_A) parents produced perhaps four calves each, while A and B cows may have had an average of five calves each.

The structure of grading-up herds

It was shown in a previous paper (Wiener, 1953) that, because of the hierarchical structure of the Ayrshire breed, the genetically effective size of the breeding population is small compared with the total size. It is now found that none of the herds at the top of the breed hierarchy (in 1946) register cows in the Appendix. None-the-less, grading-up may form the conscious breeding policy of other herds selling bulls. To this end the data were analysed to show the structure of the grading-up herds and the relationship between grading-up, bull breeding and geographical location.

It is not easy to decide on a workable definition of a grading-up herd viewed as a breeding unit. Obviously, herds registering only an occasional Appendix or P_A female do not come into this category; but it was found (Wiener, 1950) that an appreciable proportion of herds, but very few grade animals, are excluded by arbitrarily defining a grading-up herd as one in which are registered (in any one volume of the *Herd Book*):

(*a*) Two or more females in grade B, or

(*b*) Two or more females in grade A, or

(*c*) Four or more females in grade P_A, or

(*d*) One or more females in each of two or three different grades.

Grading-up herds were selected on this definition for Table 2; the herds referred to as 'pedigree' have no P_A, A, or B animals. From Table 2 some striking differences are seen both between regions and between years. Thus, a larger proportion of herds are classified as grading-up in Scotland than in England and Wales, and the proportion of Appendix and P_A females in such herds is greatest in the south-west of Scotland, the native region of the breed. The percentage of grading-up herds increased by about half between 1946 and 1951, but the biggest increase was in England. This seems to have been achieved by initially increasing the number of B cows (26·2 % in English herds in 1946) which led to a corresponding increase in the other grades (A and P_A) as seen 5 years later. The fact that the proportion of B cows in grading-up herds had declined sharply in 1951, suggests that the rate of grading-up is waning. The decrease in the average number of females registered per grading-up herd in 1951 compared with 1946 is in line with similar results from the pedigree population. It is interesting, if somewhat puzzling, that grading-up seems to have played a much smaller part in Ayrshire breed expansion in England and Wales, where the relative expansion of this breed has been greatest (Wiener & Yao, 1952). Perhaps opportunity, in the form of a larger non-pedigree Ayrshire population from which to start, and traditional belief in the worth of the Ayrshire cow, favours grading-up in Scotland.

The proportion of herds registering bulls was found to be not very different in grading-up herds (as defined above) and pedigree herds, but there was a general decrease in the percentage registering bulls between 1946 and 1951. In 1946, about 58 % of herds registered bulls in both types of herd and around 35 % in 1951. Substantial disparity between regions existed only for pedigree herds in 1951 when more than twice as big a proportion (46·3 %) registered bulls in south-west Scotland as in England and Wales (19·8 %); all herds in 1946 and grading-up herds in 1951 showed remarkable concordance between regions in respect of bull registration. In 1946 the ratio of pedigree (P) females to males registered was practically the same (3·2) in pedigree and grading-up herds, but in 1951 had changed to 5·8 in the former and 7·4 in the latter type of herd.

Though superficially, therefore, the pedigree and grading-up herds have similar bull breeding habits, it would be necessary to delve into the pedigrees of the bulls registered to find evidence of selection for or against Appendix animals—apart from the discrimination imposed by regulation. Table 3 shows what happened in the pedigrees of 200 Ayrshire females picked at random from the *Herd Book* for 1947 (vol. 71).

It is seen (Table 3) that appreciably more Appendix cows appear on the dam's side of the pedigree than on the sire's. By regulation, none can appear as mothers of the sires themselves (genera-

Table 2, *Lactation and structure of grading-up herds in* 1946 *and in* 1951

				Grading-up herds				
		Total no. of herds registering ♀♀	% grading-up herds	Av. no. ♀♀ per herd	% of ♀♀ in each class			
Year	Region				P	P_A	A	B
1946* (vol. 69)	S.W. Scotland†	837	18·8	21·8	38·3	17·2	20·6	23·9
	Rest of Scotland	214	17·8	17·9	58·8	11·6	8·8	20·8
	England and Wales	805	7·8	18·5	58·3	3·4	12·0	26·2
1951* (vol. 76)	S.W. Scotland†	81	22·2	12·7	34·7	29·8	24·1	11·4
	Rest of Scotland	33	33·3	16·7	56·5	14·7	13·0	15·8
	England and Wales	124	17·7	5·6	58·4	11·2	21·2	9·3

* 1946, based on all *Herd Book* entries; 1951, based on a random sample of herds.
† Including the counties Ayrshire, Bute, Dumfries, Kirkcudbright, Lanark, Renfrew and Wigtown.

Table 3. *Distribution of Appendix A dams in the ancestry of a random sample of* 200 *pedigree females from vol.* 71 (1947)

	No. of dams in Appendix A		
No. of generations removed from reg. ♀♀ in vol. 71	On dam's side of sample ♀♀	On sire's side of sample ♀♀	% of 'outside' genes that have entered sample ♀♀ from Appendix A dams in their ancestry
1	15	—	0·94
2	12	0	0·38
3	7	2	0·14
4	12	10	0·17
Total			1·63

tion 2), but this does not apply further back. But for a conscious avoidance of Appendix ancestry, their number might have been the same on both sire's and dam's side of the pedigree. The dams of dams have about twice as much 'outside' blood as the dams of sires. Other, unpublished, information suggests that sampling errors may affect the individual numbers but not the general conclusion. The last column of Table 3 shows the percentage of 'outside' genes which can, on average, be ascribed to the sample females on the assumption that A cows contain 25 % 'outside' genes (i.e. genes not coming from the pedigree Ayrshire population). The most striking thing about the total figure of 1·63 % is the large part of it which is due to Appendix cows in the parental and grandparental generation (1·32 %). It is at these points that discrimination by regulation and by farmer's selection are most effective and appear to operate in the registration of bulls.

Milk and fat yield

The foregoing has shown that the grading-up process does permeate the pedigree population, albeit in small measure. It now becomes pertinent to ask what effect this influx has.

As mentioned earlier, entry into the *Herd Book's* Appendix B depends, amongst other things, on each cow reaching a specified yield of milk and fat. The simplest way in which to find out whether the selection practised to produce B cows is, in some measure, a genetic selection, is to compare the yield of the daughters of these cows with their pedigree contemporaries in the same herd. The method of obtaining this information was described above.

The sample, which included 310 herds and 1837 first-lactation heifers of the three classes—A, P_A and P—was of course divided amongst herds which were represented by any two, or all three, categories. However, the four possible types of herd each told the same story in respect of the differences of yield between the three classes; they have therefore been pooled in Table 4. The average milk yield for all animals was 7561 lb. and the average fat yield 300 lb. The average age at calving was about 31 months and the average lactation length about 280 days. Differences between the average yield of all animals of a particular class in each herd were weighted for the number of animals in that particular class (the weighting factor was $(n_1 n_2)/(n_1+n_2)$, where n_1 is the number in one class and n_2 the number in another class within the same herd). The difference in yield of milk and fat between the Appendix A heifers and their pedigree (P) contemporaries in the same herds (375 lb. milk, 13·8 lb. fat) is statistically significant ($p=0{\cdot}02$). This yield difference is associated with a small difference in age at first calving and in length of lactation. Appendix A animals calved on average 10 days later than their P contemporaries (when the comparison was made within herd). However, the association of yield with age at calving for the 806 heifers in this comparison is quite insignificant ($r=-0{\cdot}0169$). It might, however, be of interest to mention that the regression of yield on age at calving for these animals showed a decrease in yield of about 1 gal. of milk in the first lactation for every month by which calving was delayed. In respect of lactation length, the A animals were milked on average for 283 days and the P animals for 277 days. When the within-herd difference is weighted for number of animals it is found to be 7 days. At the same time there is no difference in lactation length between P_A and A heifers.

Table 4. *Contemporary comparison, within herd, of the yield of three classes of first lactation Ayrshire heifers*

	A−P	A−P_A	P_A−P
No of heifers	806	667	1108
No of herds	151	144	198
Weighted mean difference in milk yield (lb.)	375·0	217·4	−23·1
S.E. of difference	149·6	144·2	126·6
Weighted mean difference in butterfat yield (lb.)	13·78	7·81	−1·69
S.E. of difference	5·86	5·73	5·02

There is no accurate way of determining how much of the extra yield of A heifers is accounted for by the extra week in milk, without knowing the shapes of the lactation curves for the animals concerned. From an estimate of linear regression of yield on lactation length ($b_{YD}=26{\cdot}7$ lb., for 91 herds with P, P_A and A animals) the extra week would account for about half the yield difference between A and P heifers. But in any case, the longer lactation length of A heifers could well be genetic in origin, particularly since their dams tend to lactate for a long time and may thus be selected for persistency as well as for quantity of milk yield. (The average length of the qualifying lactation of B cows was 375 days for a sample registered in 1948, the last year in which such information was published.) An appreciable part of the difference in yield between contemporary A and P heifers, therefore, is likely to be genetic unless the assumption is made that A animals are treated better than their P contemporaries, and for this there seems to be no justification.

Unfortunately, the differences shown in Table 4 are not strictly additive. Thus, whilst A heifers are on average about 217 lb. better in yield than P_A heifers, the latter have a yield virtually the same as P heifers (23 lb. less), although for each class the difference ought to be about halved (assuming an

additive system and an average sample of sires). But large standard errors attach to these yield differences which make the 'discrepancies' not surprising.

DISCUSSION

The grading-up process has been material in increasing the size of the pedigree Ayrshire population. If one considers the last 30 years, say, apart from the earlier history of the breed, the cumulative registrations show that by 1952 something like 6 % of the pedigree registrations have A dams, and something of the order of 5 % of the remaining pedigree females owe their existence to the grading-up system. The total of about 11 % is comparable with the 'not more than 12 %' of the pedigree Friesian cattle population registered in 1947, which was found by Robertson & Asker (1951) to owe its existence to 'grades'. It may well be, of course, that the expansion in Ayrshire numbers could have been effected equally by registering a larger number of calves from pedigree cows.

What of a possible change of gene frequency in the pedigree population in consequence of grading-up? It is very likely that by the time an animal reaches the Appendix B stage, it will resemble pure Ayrshires in genotype to a large extent—more at any rate than would be inferred from one top cross with a pedigree bull. The same set of bulls were found, on average, to be the fathers of the A and P heifers used in the yield comparison. It seems certain therefore that any genetic superiority suggested for A heifers is due to selection of their dams, the B cows. The genetic superiority of these B cows over their own pedigree contemporaries must, in turn, be assumed to approach 72 gal., if that of their daughters approaches 36 gal.

From what has been said with regard to yield and to the selection against Appendix cows in bull breeding, it is unlikely that the genetic consequences of grading-up on the Ayrshire breed extend much beyond the Appendix A stage. But short-lived though the yield advantage of 'grading-up' may be, it does highlight the fact that some of the large amount of variation in yield obtaining within herds could be turned to good account by the selection of genetically superior breeding stock, particularly dams of bulls. In ninety-one of the herds whose yield was analysed earlier (those with P, P_A and A heifers in the same herd), some 69 % of the total variation in milk yield was within herds, and the remaining 31 % was accounted for as variation between herds (the within-herd standard deviation for milk yield among the 744 animals concerned was 169 gal.). Robertson & McArthur (1955) have pointed out that possibly no more than 10 % of the milk yield variation between herds is genetic in origin compared with some 25 % or so of that within herds. But, as seen from the studies on breed structure and migration, the potentialities of selection within herds are little heeded in general. Mahadevan (1951) calculated a genetic superiority of dams of bulls in twelve leading Ayrshire herds to be 35 gal. for bulls sold and 40 gal. for bulls retained in the herd. The average yield of Mahadevan's herds was around 1000 g. of milk. Rendel, Robertson & Alim (1951) showed that in some high-yielding Ayrshire herds (studied among twenty-two herds of seven breeds) the dams of eleven bulls kept in the herds were 6·4 gal. genetically superior to their contemporaries and the dams of seventy-one bulls sold were 11·1 gal. better. In the same herds the genetic superiority of cows from which heifers were bred was 1·1 gal. only.

The selection practised on potential dams of A heifers cited in the present study appears to be higher than that practised in the other cases quoted. On an additive model the genetic superiority (I_G) depends on the selection differential in terms of standard deviations ($\bar{i}$), the heritability (h^2) and the phenotypic standard deviation (σ_P). Thus, $I_G = \bar{i}h^2\sigma_P$ (see Rendel & Robertson, 1950). For herds in this study, a genetic superiority of milk yield of 72 gal. could be inferred for B cows; the standard deviation was 169 gal. Assuming a heritability of 25 % and normal distribution of phenotypes, the B cows would be selected from the top 11 % of their herds. Obviously this estimate will depend on the validity of the assumptions, but it does not seem unreasonable in practical terms.

In the grading-up process, however, the superiority of A heifers is bought at the price of an increased generation interval. The fact that their mothers have more than an average number of registered offspring, and are themselves not selected in some cases until late in life, ensures this. Perhaps one might be tempted in the light of the grading-up story, to recommend selection of dams of bulls by, say, a qualifying yield. Such a recommendation, however, would need to be tempered by the thought that the annual rate of genetic improvement is as much a function of the generation interval as of the genetic superiority of the breeding stock.

SUMMARY

The grading-up system, in the Ayrshire Cattle breed, whereby the descendants of non-pedigree cows enter the registered (*Herd Book*) population, is studied principally from three aspects: (1) its numerical importance in the population; (2) the breeding structure of herds practising grading-up, and (3) the possible genetic effect of grading-up on milk and fat yield.

Cows at various stages of grading-up are noted

in an Appendix to the *Herd Book*. The numerical importance of the grading-up system has varied with the rate of expansion of the breed as a whole—being greatest during the most rapid expansion—but, at all times, Appendix cows have had more registered female offspring than have pedigree cows. The volume of grading-up was regulated by the number of cows in Appendix B. Some 6 % of the pedigree females registered in the last 30 years have Appendix A mothers and a further 5 % or so owe their existence to grading-up during the last 30 years.

On average, the proportion of herds registering bulls is not greatly different among the herds which grade-up and those which do not. Similarly, the ratio of males to pedigree females registered was about the same in both types of herd. None-the-less, there appears to be considerable selection against Appendix animals in the ancestry of bulls compared with cows, and none of the large bull-breeding studs appear to pursue a grading-up policy. A greater proportion of Ayrshire herds were grading-up in Scotland than in England.

Entry into Appendix B of the *Herd Book* is confined to cows reaching a qualifying yield. The daughters (A) of these B cows mated to unselected pedigree bulls were found to yield significantly more in their first lactation (36 gal. milk and 14 lb. butterfat) than contemporary pedigree Ayrshire heifers in the same Scottish milk recorded herds in 1955. Part, if not all, of this superiority is thought to be genetic.

Among the 744 heifers of ninety-one milk recorded Scottish Ayrshire herds, 69 % of this variation in milk yield was within herds, and the within herd standard deviation in milk yield was 169 gal. The possibilities of selection for yield within herds are discussed.

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Population dynamics in fourteen lowland breeds of sheep in Great Britain

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Vital statistics of fourteen breeds of sheep presented in this paper are intended as background information for the development of breeding plans. Many factors have a bearing on such plans, but only those associated with breed structure are studied here. They include the numerical size of breeds and of individual flocks, the number of years that flocks remain in existence, the geographical distribution of breeds and the amount of interchange of breeding stock between flocks. The shape of the structure is determined by the extent to which flocks within a breed have become organized into a hierarchy.

Such matters have hitherto been examined in some detail for breeds of cattle and pigs, but not for sheep—although two aspects, flock size and duration, were discussed for a number of breeds in a preliminary report by Wiener (1954).

MATERIAL AND METHODS

The breeds studied are: Clun Forest, Devon Closewool, Dorset Down, Dorset Horn, Hampshire Down, Kent or Romney Marsh, Leicester, Lincoln, Oxford Down, Ryeland, Shropshire, South Devon, Southdown and Suffolk. The source of information is the published flock book of each Breed Society. The suitability of the flock book, in terms of adequate flock returns and pedigree information, was the only criterion in the choice of breeds for this study. Not all the books gave information on all the desired aspects but the following data were noted for each flock wherever possible. (1) Flock size in terms of the number of breeding females. (2) Age of flock in terms of the number of years registered or established. (3) Number of stock rams used and whether home-bred or purchased. (4) Number of ram lambs individually registered. (5) Origin of the sires of individually registered rams. (6) Geographical location of the flock.

All the flocks entered in each flock book were considered. For some breeds the survey was extended over more than 1 year's returns, thus providing an indication of changes in flock attributes with time.

RESULTS

Flock size

Data based on a recent volume of the flock book for each breed are summarized in Table 1. In most of the breeds involved, females are not normally mated for the first time until they are about

Table 1. *Flock size*

Breed	Flock book volume	Flock return for the year	No. of flocks	Average no. breeding ♀♀	% of flocks according to no. of breeding ♀♀				
					1–50	51–100	101–200	201–300	> 300
Clun Forest*	33	1956	712	153	19·4	21·8	31·9	15·4	11·5
Devon Closewool	35	1957	273	210	5·9	11·7	35·9	27·8	18·7
Dorset Down	49	1956	92	123	34·8	15·2	29·4	16·3	4·3
Dorset Horn	66	1956	104	101	41·3	21·2	24·0	10·6	2·9
Hampshire Down	69	1957	87	105	42·5	23·0	14·9	9·2	10·4
Kent or Romney Marsh	63	1957	74	173	20·3	20·3	36·5	14·8	8·1
Leicester	62	1953	110	58	59·1	30·9	8·2	0·9	0·9
Lincoln	67	1957	29	66	41·4	41·4	17·2	—	—
Oxford Down	70	1957	106	47	70·8	17·0	11·3	—	0·9
Ryeland	39	1954	33	28	81·8	15·2	3·0	—	—
Shropshire	72	1956	32	63	53·1	25·0	21·9	—	—
South Devon	54	1956	118	61	48·3	39·8	11·9	—	—
Southdown	67	1957	87	64	54·0	26·4	17·3	2·3	—
Suffolk*	73	1958	792	38	81·2	12·1	4·7	1·6	0·4
All 14 breeds	—	—	2649	92	46·2	18·9	19·5	9·3	6·1

* Ewe hoggs included in number of breeding females.

18 months old. In a few breeds, however, it is customary to mate ewe lambs. Flock size is reckoned in terms of breeding females—ewes alone, or ewes plus ewe lambs as appropriate.

There is considerable variation in flock size between breeds as well as within breeds. For the 2649 flock returns examined almost two-thirds are of flocks with less than 100 breeding females and only 15 % with over 200, but nearly 50 % of all the breeding females in the survey are included in these larger flocks. These grand totals are, however, weighted heavily by the Clun Forest and Suffolk breeds which account for over half the total flocks in the survey. The largest 10 % of flocks in each breed contain, on average, 29 % of all the breeding females; and the small flocks in each breed account for half the number of flocks but for only about 20 % of the ewes.

Flock age

This is given in the flock books of eleven of the fourteen breeds. Except for the Oxford Down breed, the age shown in Table 2 represents the number of years of registration with the Breed Society. For Oxford Down flocks the information given is as the number of years since establishment—presumably longer than the period since first registration but by an amount which it is difficult to assess. The flock books of three breeds give information on both the year of establishment of each flock and the year (or the volume of the flock book) when registration first took place. Flock 'age' calculated from the two sources differs by only 7 months for Suffolk flocks but by 9 years for Kent or Romney Marsh flocks and by 16 years for South Devon flocks.

The frequency distribution shows that a large proportion of flocks are less than 5 years old and only a minority over 20

Number and source of stock rams and number of ewes per ram

Table 3 shows that a large proportion of flocks, about a third, used one ram only, while less than 10 % of all flocks used five or more rams. But whilst the single-ram flocks accounted for 14 % of all the stock rams in use, the flocks at the other end of this scale employed 26 % of the rams. A proportion of flocks—large only in the Dorset Down breed—showed no record of rams used; these may be accidental omissions, or flocks whose ewes were served by rams recorded in other flocks. On average, 13 % of the rams used were 'home-bred' which is here defined as meaning the proportion of rams which bore the same flock prefix as the flocks in which they were used. The prefix indicates the breeder of a ram but says nothing about the pedigree. The home-bred proportion varied between breeds from 4 % (South Devon) to nearly 40 % (Kent or Romney Marsh). The proportion of home-bred rams used increased by a steady progression with the number of rams used per flock from an average of 2·9 % for single-ram flocks to 25 % for flocks using five or more rams.

Whereas the various breeds (with the exception of the Kent or Romney Marsh breed) did not differ greatly in the average number of stock rams used per flock (2·3) they did differ very appreciably from each other in the average number of ewes per ram. Clun Forest breeders, for example, mated, on average, more than three times as many ewes to each ram as did Suffolk breeders (see Table 4). Within each breed the picture is interesting but complicated. Thus the average number of ewes per ram is fairly constant when flocks are classified by the number of rams used. However, when flocks are classified by flock size, the average number of ewes per ram increases steadily with flock size range

Table 2. *Flock age*

Breed*	No. of flocks	Average no. of years registered	% of flocks according to no. of years registered			
			1–5	6–10	11–20	> 20
Devon Closewool	273	13·5	30·8	20·5	23·4	25·3
Dorset Down	92	14·6	40·2	12·0	23·9	23·9
Dorset Horn	104	13·4	45·2	13·5	20·2	21·1
Hampshire Down	87	14·2	49·4	16·1	15·0	19·5
Kent or Romney Marsh	74	15·1	25·7	16·2	37·8	20·3
Leicester	110	16·0	25·4	21·8	26·4	26·4
Lincoln	29	21·8	10·4	27·6	17·2	44·8
Oxford Down†	106	18·7	15·1	23·6	33·0	28·3
South Devon	118	13·3	25·4	25·4	32·2	17·0
Southdown	87	9·5	71·3	10·3	5·8	12·6
Suffolk	792	8·5	54·4	18·5	16·0	11·1
All 11 breeds	1872	11·9	42·7	18·6	20·7	18·0

* Flock book volume and year as in Table 1; no information available on flock age for three breeds, viz. Clun Forest, Ryeland, Shropshire.

† Number of years since establishment of flock.

(Table 4). This arises in part because even the smallest flocks have at least one ram, but mainly because of large variation in the number of rams used by flocks within each size range, combined with a skewness of distribution (flock size plotted against the ram numbers) which changes with the number of rams used and with flock size. Thus many small flocks, though not a majority, use several rams—more than apparently needed for purely reproductive purposes—whilst many large flocks mate more ewes per ram than the breed average would lead one to suppose.

In Table 4, the first three columns of figures, showing the number of flocks and the overall breed averages, refer to all flocks in each breed including those not recording the number of rams used, whereas all other columns refer only to flocks making returns of the number of rams they have used.

Breed structure

The most reliable method of ascertaining the relative genetic importance of different herds or flocks in a breed is by pedigree analysis over a number of generations. This procedure is, however, not merely laborious but open to criticism where, as in many breeds of sheep, individual registration of animals is restricted to a selected few.

Table 3. *Number of stock rams used and proportion home-bred*

Breed*	No. of flocks	% of flocks according to no. of rams: 0	1	2	3	4	5 or more	Total no. of rams	Home bred (%)
Clun Forest	712	9·0	25·0	26·5	18·3	11·4	9·8	1715	11·4
Devon Closewool	273	2·2	13·6	33·7	30·0	12·4	8·1	724	5·4
Dorset Down	92	30·4	14·1	16·3	12·0	10·9	16·3	203	20·2
Dorset Horn	104	7·7	28·8	26·0	18·3	7·7	11·5	253	11·9
Hampshire Down	87	1·1	25·3	28·8	9·2	16·1	19·5	263	23·2
Kent or Romney Marsh	74	0	13·5	20·3	13·5	13·5	39·2	397	39·8
Leicester	110	0	40·0	40·0	10·0	4·5	5·5	219	8·7
Lincoln	29	10·3	38·0	20·7	10·3	13·8	6·9	58	10·3
Oxford Down	106	0	38·7	34·0	14·1	4·7	8·5	245	Not shown
Ryeland†	*33*	*6·1*	*33·3*	*30·3*	*15·1*	*6·1*	*9·1*	*80*	*28·8*
Shropshire	32	3·1	43·8	31·2	9·4	9·4	3·1	61	13·1
South Devon	118	0	58·5	33·9	5·9	0	1·7	180	4·4
Southdown	87	1·1	42·5	32·2	12·7	8·0	3·5	171	13·5
Suffolk	792	0	44·7	31·7	12·5	5·7	5·4	1622	11·4
All 14 breeds	2649	4·3	32·9	29·8	15·6	8·6	8·8	6191	13·4‡

* Flock book volume and year as in Table 1.
† Rams used over a 2-year period.
‡ Average % for 13 breeds (excluding Oxford Down).

Table 4. *Number of ewes per stock ram*

Breed*	No. of flocks	Average no. of rams per flock	Average no. of ewes per ram‡	No. of ewes per ram according to no. of rams per flock: 1	2	3	4	5 or more	No. of breeding ♀♀ per flock: 1–50	51–100	101–200	201–300	>300
Clun Forest	712	2·4	64	60	59	58	61	55	25	44	56	69	73
Devon Closewool	273	2·7	79	74	78	78	76	80	24	52	67	81	96
Dorset Down	92	2·2	56	31	46	36	49	44	21	32	46	48	60
Dorset Horn	104	2·4	42	24	36	44	46	45	18	36	43	50	60
Hampshire Down	87	3·0	35	23	25	35	35	41	16	28	38	48	43
Kent or Romney Marsh	74	5·4	32	33	36	34	29	32	22	27	28	35	38
Leicester	110	2·0	29	22	31	27	29	33	19	33	37	37	67
Lincoln	29	2·0	33	46	37	30	28	21	27	36	30	—	—
Oxford Down	106	2·3	20	22	23	16	23	19	15	17	35	—	52
Ryeland†	*33*	*2·4*	*12*	*15*	*15*	*7*	*11*	*10*	*11*	*12*	*13*	—	—
Shropshire	32	1·9	33	33	38	29	32	26	27	34	38	—	—
South Devon	118	1·5	40	47	37	35	—	24	32	46	42	—	—
Southdown	87	2·0	32	30	31	30	41	33	18	35	45	42	—
Suffolk	792	2·1	19	20	17	15	19	24	13	26	33	32	42

* Flock book volume and year as in Table 1.
† Rams used over a 2-year period.
‡ Including flocks not recording number of rams.

It has been shown in cattle studies (Wiener, 1953) that a simplified approach can be used to classify herds roughly according to genetic importance in their breeds. This method relied on a single volume of the herd book and took into account (1) the type and number of registrations made for each herd, and (2) the extent to which each herd featured among the sires of registered bulls. This simplified approach has also been adopted in the present paper. In ten of the fourteen breeds studied the regulations stipulate that rams used in registered flocks must have their individual pedigrees recorded. In only these breeds are both requirements met for dividing flocks into a hierarchy of importance.

Table 5 gives an indication of the extent of the hierarchy and presents some features of the flocks in each of the four classes recognized. The terminology is adapted from (though not the same as) that used by Wiener (1953). Flocks which supplied the sires of registered rams were called 'Breeders'' flocks and they were subdivided into two groups according to their importance as suppliers of rams to other ram breeders. The subdivision adopted (as providing a common denominator independent of the numerical size of the breeds) was between those flocks which had

(i) supplied the sires of approximately 75 % of the registered rams (other than home-bred rams) and

(ii) supplied the sires of the remaining 25 % of registered rams (other than home bred rams).

Flocks which are not included above were termed 'Multipliers'' flocks and were subdivided according to whether they (i) registered rams, or (ii) did not register rams. Some flocks which registered rams undoubtedly had some of these used in other pedigree flocks even though their names did not appear among the sires of registered rams. This group of flocks has not been separately studied and has been included among the 'Multipliers''.

Table 5 shows that the proportion in the 'top' group ('Breeders' flocks (i)) varied from 2·1 % (Clun Forest and Suffolk) to 21·9 % (Shropshire) and was inversely associated with the number of flocks in the breed (rank correlation of 0·88). But the absolute size of this group of flocks—whose rams sired 75 % of the registered males—was not nearly as different as the difference in the numerical size of the breeds might have led one to suppose. Thus while the Suffolk breed population consisted of about twenty-eight times as many flocks as the Lincoln breed the 'top' group was only about four times as large. It can also be seen that a majority of flocks ('Multipliers'' (ii)), except in the Kent or Romney Marsh and Ryeland breeds, did not register rams. Ram lambs which are not selected for registration are presumably destined for use in non-pedigree flocks, or for crossing purposes, or for the butcher.

Table 5. *Breed structure*

	Type of flock†	Breed*									
		Clun Forest	Hamp-shire	Kent or Romney Marsh	Leicester	Lincoln	Ryeland	Shrop-shire	South Devon	South Down	Suffolk
Total no. flocks		712	87	74	110	29	33	32	118	87	792
Percentage of flocks	'Breeders'' (i)	2·1	5·7	10·8	6·4	13·8	9·1	21·9	6·8	4·6	2·1
	'Breeders'' (ii)	6·7	9·2	17·6	5·4	13·8	12·1	3·1	12·7	11·5	8·4
	'Multipliers'' (i)	21·7	9·2	31·1	15·5	6·9	51·5	0	20·3	28·7	21·5
	'Multipliers'' (ii)	69·5	75·9	40·5	72·7	65·5	27·3	75·0	60·2	55·2	68·0
Av. no. of ewes per flock	'Breeders'' (i)	229	282	171	90	106	35	109	63	147	136
	'Breeders'' (ii)	209	261	351	59	68	57	43	74	113	56
	'Multipliers'' (i)	189	51	173	87	98	27	—	63	63	53
	'Multipliers'' (ii)	134	86	96	48	54	14	51	58	26	28
Av. age of flocks (years)	'Breeders'' (i)	—	46	28	37	41	—	—	29	28	27
	'Breeders'' (ii)	—	21	21	31	9	—	—	15	17	16
	'Multipliers'' (i)	—	5	15	18	9	—	—	14	8	10
	'Multipliers'' (ii)	—	12	9	12	18	—	—	11	7	6
Percentage of home-bred sires used	'Breeders'' (i)	43	44	45	23	27	25	35	8	44	29
	'Breeders'' (ii)	26	29	60	8	10	47	0	7	21	12
	'Multipliers'' (i)	22	38	36	15	0	28	—	3	7	24
	'Multipliers'' (ii)	2	16	1	4	4	0	0	4	9	4
Percentage of home-bred rams registered	'Breeders'' (i)	33	43	41	23	0	52	44	12	35	36
	'Breeders'' (ii)	33	29	43	39	0	55	—	10	18	11
	'Multipliers'' (i)	15	48	36	3	0	39	—	0	7	12
	'Multipliers'' (ii)	—	—	—	—	—	—	—	—	—	—
No. of rams registered per 100 ewes in flock	'Breeders'' (i)	17	8	18	7	7	28	2	22	27	10
	'Breeders'' (ii)	7	4	6	4	18	28	0	10	11	4
	'Multipliers'' (i)	3	7	5	2	6	14	—	10	16	3
	'Multipliers'' (ii)	—	—	—	—	—	—	—	—	—	—

* Flock book volume and year as in Table 1.

† 'Breeders'' flocks are those which supplied the sires of registered rams. Further subdivision is according to relative importance (see tex
'Multipliers' flocks are those not included among 'Breeders' which (i) register rams, and (ii) do not register rams.

In terms of all the other flock attributes listed—ck size, age, percentage of home-bred rams used, rcentage of rams registered which were home-ed, and number of rams registered per 100 ewes the flock—there was a steady gradation from the p of the hierarchy to the bottom. The top section 'Breeders'' flocks included on average the largest d oldest flocks using the largest proportion of me-bred rams, registering the biggest percentage ram lambs with home-bred sires and registering e largest number of rams per 100 ewes in the ck. The individual exceptions to the average nds are fairly few and occur mostly in the breeds here the number of flocks is small. It is note-rthy, however, that the actual proportion of ms registered with the home-bred label (in the ree categories of flock which register rams) was, the whole, about the same or less than the pro-rtion of home-bred stock rams used (the average rcentages for the registered rams were 34, 29, 16, d for the stock rams used 35, 39, 23). In the oice of ram lambs for registration, home-bred hers were not therefore especially favoured. The all percentages (0 to 16, average 4) of home-bred es in flocks not currently registering rams shows at the divisions of the hierarchy are not hard and t since the flocks involved must have registered ms in a preceding year.

There is a tendency (not tabulated) for the mber of ewes per ram to decrease slightly as one ves from 'bottom' to 'top' of the hierarchy in e Clun Forest, Kent or Romney Marsh, Leicester, d Lincoln breeds and for a slight reverse trend to w in the Southdown and Suffolk breeds. The r remaining breeds show what appears to be only ndom variation in this characteristic. Since the p' flocks are, on average, the larger, the stratifi-tion of flocks according to function cuts in some asure across the classification by flock size which owed clearly that the larger the flocks the fewer ms they used per hundred ewes (Table 4).

Geographical location

As breeds of sheep gain in popularity and find a che in the sheep industry, for example as a breed oducing rams for crossing with ewes of other eeds, so flocks are established in parts of the untry often far removed from the location where e breed was developed; the location, moreover, which in many cases the breed was popularly ought to have been developed. It was decided, erefore, to test the possibility that flocks in their tive' domain differ from flocks in other areas in ch attributes as numerical size and age, and in eeding habits such as the use of home-bred rams. was also intended to find out whether ram eeders were concentrated in the 'native' area (as own by the proportion of flocks registering rams) and whether these breeders, as a body, regarded the 'native' area as their principal source of rams for ram breeding.

Difficulty arose in deciding on practical limits for the 'native' area; to have considered this solely on historical grounds could have left the 'native' location with an insufficient representation of flocks for meaningful conclusions to be drawn about flock attributes. County boundaries were used for the delineation, but this too raised a problem with regard to the classification of particular flocks. It was decided, therefore, to create a category of location between the 'native' and the 'other', namely an area 'surrounding' the native county or counties. The counties included in each area are shown in a footnote to Table 6. Five breeds were chosen for division according to location; all five, but particularly the 'Down' breeds, are long established breeds and are sufficiently widespread in their distribution for division to be worthwhile.

The percentages of flocks in each location are partly a consequence of the arbitrariness of the divisions drawn, but also show how some breeds have spread out geographically more than others. The Oxford Down and Suffolk breeds in particular, both used widely in crossing with other breeds, each had only a small proportion of flocks in the 'native' location; these two were also the only two of the five breeds which were significantly represented in Scotland and Ireland (although these two countries showed some differences from each other in flock attributes, both were included in 'other' locations).

In terms of numbers of ewes, flocks in the 'native' location were consistently the largest and, with the exception of Southdown flocks, smallest in the 'other' regions. The 'other' region for Southdowns includes, however, the counties bordering Cambridgeshire which ranked in the breed history next only to Sussex as a centre in the development of the breed. Cambridgeshire itself was without registered Southdown flocks in the year studied but the thirteen flocks in the bordering counties averaged eighty-six females—about the same as did flocks in Sussex.

Flock age was on average highest in the 'native' areas and lowest in the 'others' except for the Southdown breed (as a matter of interest, the average age of Southdown flocks in counties bordering Cambridgeshire was 16 years—higher than in the 'native' Sussex).

The trends shown by flock size and age in respect of location are reflected in the proportions of flocks which register rams. For the Oxford Down, Southdown and Suffolk breeds, this proportion was highest in the 'native' areas and in all five breeds studied it was lowest in the 'other' regions.

The other characteristics listed in Table 6 did not show consistent differences between locations when

Table 6. *Breed distribution by geographical location*

Breed*	Total no. of flocks	Location of flocks†	Flocks (%)	Av. no. ewes per flock	Av. flock age (years)	Flocks registering rams (%)	'Breeders'' flocks (%)	No. of registered rams per 100 ewes	Home-bred sires used (%)
Clun Forest	712	Native	45·2	168	—	33	11	2·3	11
		Surrounding	17·6	152	—	35	13	3·0	18
		Others	37·2	135	—	25	4	1·2	8
Hampshire Down	87	Native	20·7	170	26	28	11	1·5	18
		Surrounding	20·7	133	19	33	22	4·1	29
		Others	58·6	72	9	20	14	1·9	22
Oxford Down‡	106	Native	10·4	111	30	55	—	0·7	—
		Surrounding	34·9	56	20	41	—	0·9	—
		Others	54·7	30	16	31	—	1·1	—
Southdown	87	Native	29·9	88	10	50	19	6·2	11
		Surrounding	31·0	51	10	44	7	12·6	11
		Others	39·1	55	9	32	18	11·5	18
Suffolk	792	Native	2·8	138	17	68	41	3·6	30
		Surrounding	3·2	99	14	28	20	2·2	12
		Others	94·0	33	8	28	8	2·0	10

* Flock book volume and year as in Table 1.

† The following divisions are described in more detail in the text; 'other' locations include those counties not specifically named (in England and Wales) and the whole of Scotland and Ireland.

Clun Forest breed	'Native' counties	Hereford and Shropshire
	'Surrounding'	Brecon, Gloucester, Monmouth, Montgomery, Radnor, Stafford, Worcester
Hampshire Down breed	'Native' counties	Hampshire and Wiltshire
	'Surrounding'	Berkshire, Devon, Dorset, Gloucester, Somerset, Surrey
Oxford Down breed	'Native' counties	Oxford, Gloucester, Buckingham
	'Surrounding'	All other counties of England and Wales
Southdown breed	'Native' county	Sussex
	'Surrounding'	Berkshire, Buckingham, Hampshire, Kent, Oxford, Surrey
Suffolk breed	'Native' county	Suffolk
	'Surrounding'	Cambridge, Essex, Hertford, Norfolk

‡ No information available on 'Breeders'' flocks and percentage home-bred sires used.

considered across breeds but showed differences separately for each breed. For example, in the Suffolk breed clearly the largest proportion (41 %) of 'Breeders'' flocks was in the 'native' region; both among Suffolk and Clun Forest flocks only a small percentage of 'Breeders'' was found in the 'other' locations.

The percentages of home-bred rams used was, in the Suffolk breed, also greatest (30 %) in the county of Suffolk itself and the percentage was lowest both in the Suffolk and Clun Forest breeds for the 'other' regions. The number of rams registered per 100 ewes showed a trend in the Suffolk breed alone. In the other four breeds, although the number of rams registered per hundred ewes was not consistently lower in 'other' locations, the differences in flock size between locations ensured that the number registered per flock was lowest in these 'other' regions.

Changes over a period of time

Flock books of the Oxford Down, Shropshire, Southdown and Suffolk breeds were examined for a number of years dating back to 1911. All the other breeds except the Clun Forest and Ryeland were surveyed for at least one other year in the period 1945–47 (Wiener, 1954).

Flock size, in terms of the average number of ewes per flock, was the only attribute to show a consistent change—a decrease—for all breeds. It follows that breeds like the Suffolk which have greatly expanded recently in their numbers of flocks have not shown a corresponding increase in the total size of their breeding population. Probably associated with the establishment of many new flocks was the lower average flock age in the Suffolk breed (8 years old in 1959 compared, for example, with 19 years old in 1911). The same was true of the Southdown breed where detailed (unpublished) data have shown a good association between expansion and contraction in numbers of flocks and average flock age—as one increased the other fell. For the other breeds in this study taken in conjunction with each other there was no obvious change in average flock age over the last 10 or 12 years.

A hierarchy of breeders within each breed has been a consistent finding from all the flock books studied, although the actual composition of the 'top' group changes over a period of years. This change is not, however, as rapid as the general turn-over of flocks since the 'Breeders'' flocks (as defined in this paper) were on average the oldest

cks in each breed and contained among their mber some very old ones indeed. The two breeds st closely studied for the aspects of breed ucture—Southdown and Suffolk—showed an eresting difference. In the Southdown breed en flock numbers were large (e.g. 359 flocks in 11) the percentage of 'Breeders'' flocks was small %), whereas in the late 1940's and early 1950's en flock numbers were at a very low level (less an 40) the proportion of 'Breeders'' flocks stood gh (about 20 %). Thus the actual number of the p' flocks did not vary in proportion to the vari- on in total numbers—a situation analagous to at found to exist between breeds and discussed lier in the paper. In the Suffolk breed, on the her hand, the proportion of 'Breeders'' flocks was same (2·1 %) in 1911 (and almost the same in ermediate years) as in 1959. In the former year ere were 238 Suffolk flocks and in the latter 792. e most obvious reason for this breed difference is at the Suffolk breed had not declined to, in any of ese years, the small number of flocks of the South- wn breed. It may be inferred that in times of ed decline the 'top' flocks are the last to give up.

DISCUSSION

This study, which is confined to flocks registered h Breed Societies, has shown that a majority of cks, at any one time, are small, have been in stence for only a few years, use only a small mber of rams and do not breed any rams used by er pedigree breeders. Alongside these are a few ge, long-established flocks, where many rams are d and where the rams bred are in turn widely d in pedigree flocks. In genetic terms the picture ne of a majority of flocks which, if left as self- ntained units, can have little opportunity for n-random genetic advance, and a minority of cks where such opportunities exist. Non- digree flocks or flocks of a different breed can ovide facilities, for example for testing rams, ditional to those afforded by the registered flocks emselves. This survey provides no information this point; neither can it answer the question ether such opportunities as exist for genetic vance within the registered flocks are turned to vantage. The survey supplies only a few pointers. ong these may be cited (1) the degree of within- k selection as shown by the proportion of home- d rams used, (2) the intensity of selection of ns for registration as gauged by the number of h registrations per hundred ewes in the flock, d (3) the extent to which opportunities have been ght for selection between ram families as indi- ed by the number of rams used per hundred es mated. The very large differences existing tween breeds in the number of ewes put to each ram might be regarded as reflecting differences in breed purpose, for example breeds where the main purpose is to produce rams for crossing compared with those where the major income is from the production of fat-lambs or breeding ewes. This speculation is not, however, supported by evidence from within breeds where there is no corresponding difference in the number of ewes per ram between the flocks producing rams for sale to pedigree breeders and the other flocks.

It follows from the evidence of a hierarchy within each breed that any genetic change in the flocks at the top of the hierarchy will be disseminated through each breed fairly rapidly—and this deduction is in line with the evidence that has emerged from studies of breeds of cattle. It may also be inferred from the pattern of breed hierarchy that different strains are unlikely to exist within each breed unless the 'top' flocks represent not a single peak to the hierarchy, but parts of several peaks. This point has not been investigated, but the finding that the 'top' flocks were not confined to one part of the country for each breed makes the possibility of regional differentiation more feasible than if these flocks were restricted to one area.

The existence of a hierarchy within each breed leads inevitably to the thought that some in-breeding must occur on account of the restricted effective number of sires used in each breed. Except, however, in the smallest of the breeds with the smallest absolute number of 'top' flocks the actual loss of heterozygosity—using Wright's (1931) equation—is unlikely to be appreciable. In the breeds studied, it might vary between perhaps 0·1 and 0·7 % per generation if each of the 'top' flocks introduces on average two new rams per year and if the generation interval is 3 years.

Breeds are not static. The small average flock age indicates a rapid turn-over of flocks. Numbers of flocks change as do numbers of ewes. Transient fashions as well as economic circumstances alter breeders' goals. However, despite this, the evidence from studying the flock books of several years suggests that breed organization as portrayed in this paper does not greatly change.

SUMMARY

The flock books of fourteen Lowland breeds of sheep were examined to study flock size, flock age, the number and source of rams used, the extent to which flocks differ in genetic importance within their breeds, the effect of geographical location on flock attributes, and changes in breed organization over a period of time.

All breeds taken together showed that 46 % of the 2649 flocks involved had less than fifty breeding ewes and 15 % had more than 200. 43 % of flocks

were less than 5 years old and 18% were over twenty. A third of all flocks used only one ram and 9% used five or more. All breeds were found to be arranged in a hierarchy such that only a small number of flocks in each breed supplied the majority of the rams and in particular the rams used by ram-breeding flocks. The 'top' flocks were among the largest and oldest in each breed. Flocks in the 'native' region of each breed were generally larger and older than those elsewhere, but for other flock attributes the differences between regions were more peculiar to breeds. The general pattern of breed organization appeared to apply at widely differing periods of time.

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